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(*continued inside back cover*)

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UPPERMOST CENOMANIAN–BASAL TURONIAN AMMONITES FROM SALINAS, ANGOLA

By

MICHAEL R. COOPER

Cape Town Kaapstad

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By

Michael R. Cooper

Department of Geology, University of Oxford

(With 39 figures)

[*MS. accepted 18 May 1977*]

ABSTRACT

The classic ammonite locality at Salinas was visited and the section measured. Contrary to previous estimates, the earliest marine strata at this locality, resting conformably upon a fluvio-continental facies, are of latest Cenomanian age and clearly reflect marine transgression. The ammonite fauna from this locality is described, some of the more important elements being *Metoicoceras gibbosum* Hyatt, *Euomphaloceras* (*Kanabiceras*) *septemseriatum* (Cragin), *Sciponoceras gracile* (Shumard), *Calycoceras naviculare* (Mantell), *Pseudocalycoceras angolaense* (Spath), *Gaudryceras isovokyense* Collignon, *Anagaudryceras* cf. *cassisianum* (d'Orbigny), *Puzosia* (*Austiniceras*) *intermedia orientalis* Matsumoto, *Puzosia* (*Anapuzosia*) *dibleyi* (Spath), *Tetragonites* aff. *blaisoni* Collignon and *Desmoceras* (*Pseudouhlighella*) aff. *ezoanum* Matsumoto. This assemblage forms part of the world-wide *Sciponoceras gracile* Zone fauna of latest Cenomanian age. The presence of *Watinoceras coloradoense* (Henderson) and *Vascoceras* (*Paravascoceras*) cf. *cauvini* Chudeau in surface scree is taken as evidence for the basal Turonian zone of *Watinoceras coloradoense*. The Cenomanian–Turonian boundary problem is discussed at length and a modified zonation of the Lower Turonian proposed. Acanthoceratid phylogeny is commented upon, and the new subfamily Euomphaloceratinae is erected to house the following taxa: *E.* (*Euomphaloceras*), *E.* (*Kanabiceras*), *Kamerunoceras*, *Schindewolfites*, *Yubariceras*, *Romaniceras* (including *Proromaniceras*), *Obiraceras*, *Shuparoceras* and, tentatively, the Cenomanian *Tunesites*.

CONTENTS

INTRODUCTION

Salinas is situated a short distance to the north-west of the army camp of Posto de São Nicolau, 110 km to the north of Moçâmedes (Fig. 1). Douvillé (1931) was the first to describe ammonites from Salinas when he recorded a 'Barremian' to 'Turonian' fauna, identifying the following species:

Ann. S. Afr. Mus. **75** (5), 1978: 51–152, 39 figs.

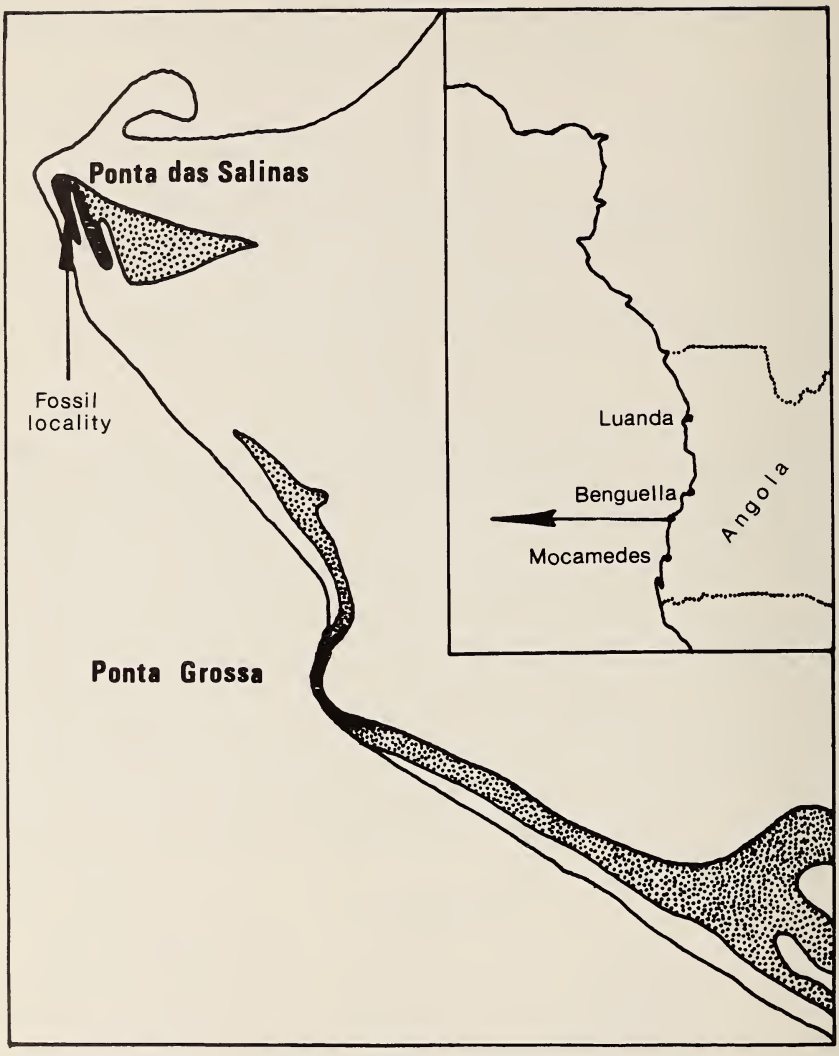

Fig. 1. Locality map.

Puzosia matheroni d'Orbigny	Barremian
Pulchellia caicedoi Karsten	
Acanthoceras lyelli Leymerie	Albian
Desmoceras toucasi Jacob	Vraconnian
Knemiceras uhligi Choffat	
Acanthoceras borgesi Douvillé	Cenomanian
Gaudryceras salinarium Douvillé	
Prionotropis echinatus Douvillé	Turonian

Spath (1931), in a review of this fauna, considered all these ammonites to be of Cenomanian age, referring the *Acanthoceras lyelli* to *Protacanthoceras*, *Acanthoceras borgesi* to *Metacalycoceras* and *Prionotropis echinatus* to *Neocardioceras*, while considering the *Puzosia matheroni* closer to the Cenomanian *Austiniceras dibleyi* than d'Orbigny's Lower Cretaceous species.

Haas (1942: 158, 163) tentatively referred *Desmoceras toucasi* Douvillé (*non* Jacob) to *Puzosia spathi* Venzo (=*P. venzoi* Breistroffer 1947), thereby suggesting the Cenomanian of Salinas to be underlain by Albian strata. He reasserted this opinion (Haas 1952: 16) when describing a specimen of *Desmoceras latidorsatum* var. *inflata* Breistroffer, supposedly from the Salinas exposure, stating that since 'the specimen under discussion is undoubtedly conspecific with the specimens from Egito and Catumbela, whose Albian age need not be questioned, the Albian fauna may be assumed to be present beneath the Cenomanian one at Salinas'.

Howarth (1965) followed Spath in considering the Salinas fauna to be Upper Cenomanian, but felt that *Desmoceras latidorsatum* var. *inflata* admitted to the presence of Lower Cenomanian strata at Salinas.

Kennedy (1971) considered the Salinas fauna to be of high Cenomanian or basal Turonian age, pointing out that *Metacalycoceras borgesi* (Douvillé) was conspecific with *Calycoceras naviculare* (Mantell), while confirming the puzosiid to be *Austiniceras dibleyi*. *Neocardioceras echinatum* (Douvillé) he referred to the genus *Kanabiceras*, while following Spath (1931) in considering the '*Pulchellia*' a misidentified acanthocerate. The *Stoliczkaia dispar* var. *attenuata* Douvillé (1931: 29, pl. 2 (fig. 2a–b)), if a *Stoliczkaia*, he considered must 'surely be Lower Cenomanian'.

GEOLOGY

The lowest beds in the stratigraphic succession at Salinas (Fig. 2) are exposed in the low sea-cliffs to the south of the Baia das Salinas. These beds comprise about 8 m of predominantly red, but also white, green and purple, laminated silts and clays, entirely lacking in fossils. That these beds attain a much greater thickness is evident in the sea-cliffs to the south of the Farol de Ponta Grossa, where at least 40 m of predominantly red siltstones and sandstones underlie the lowest limestone horizon.

At Salinas these beds are overlain by 1,80 m of yellowish fine-grained sandstone, also unfossiliferous, the upper 0,80 m with numerous well-rounded boulders and pebbles up to 0,20 m in diameter. This conglomeratic horizon is overlain by 1,0 m of highly fossiliferous white limestone, characterized by the abundance of the gasteropod *Pseudomelania salenasensis* Rennie.

The succession can thus be interpreted as a typical transgressive sequence with initially highly coloured, unfossiliferous lagoonal sediments covered by receding dune sands or barrier deposits, then beach conglomerates and finally shallow-water open marine limestones.

The '*Pseudomelania* Beds' are crammed with *Rhynchostreon suborbiculatum* (Lamarck) (Fig. 3), together with *Exogyra* (*Costagyra*) *olisiponensis* Sharpe,

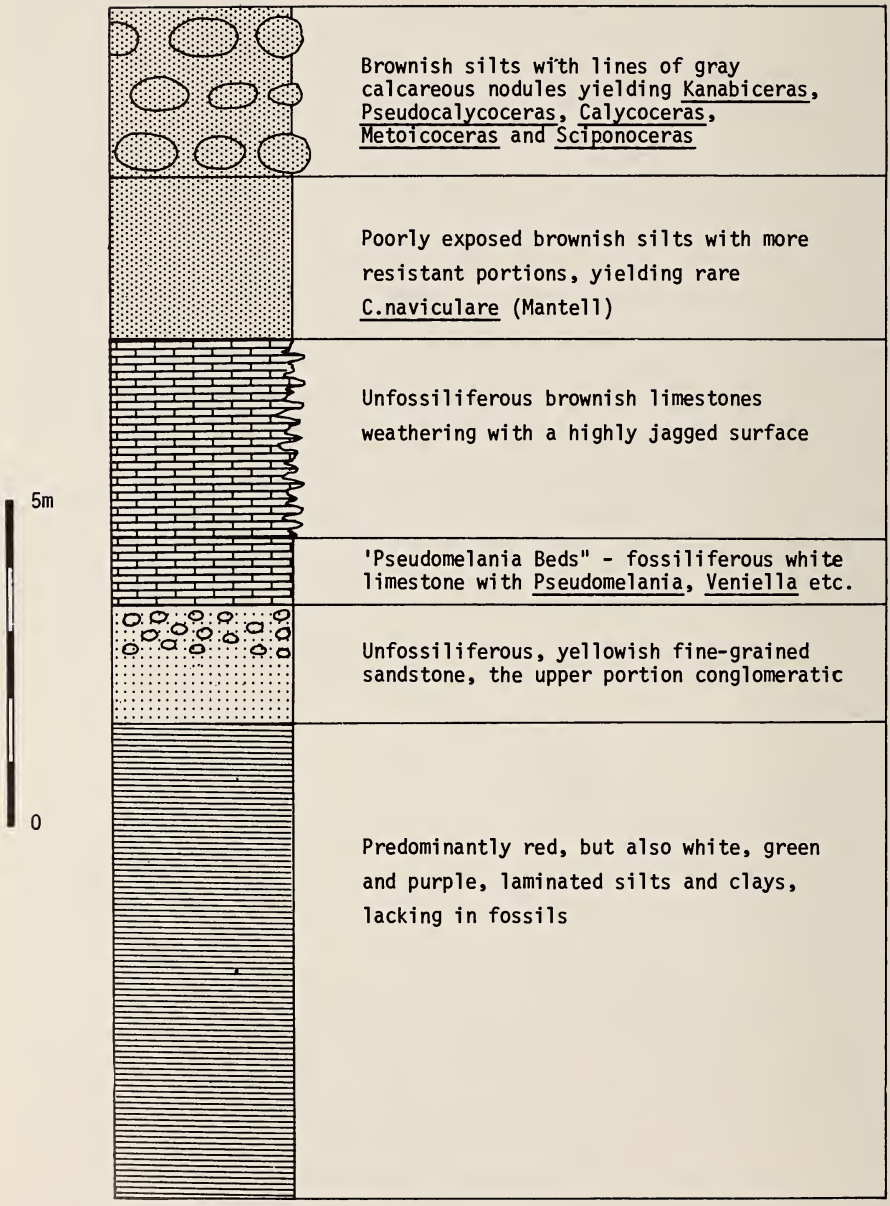

Fig. 2. Geological section through the Salinas exposure. For explanation see text

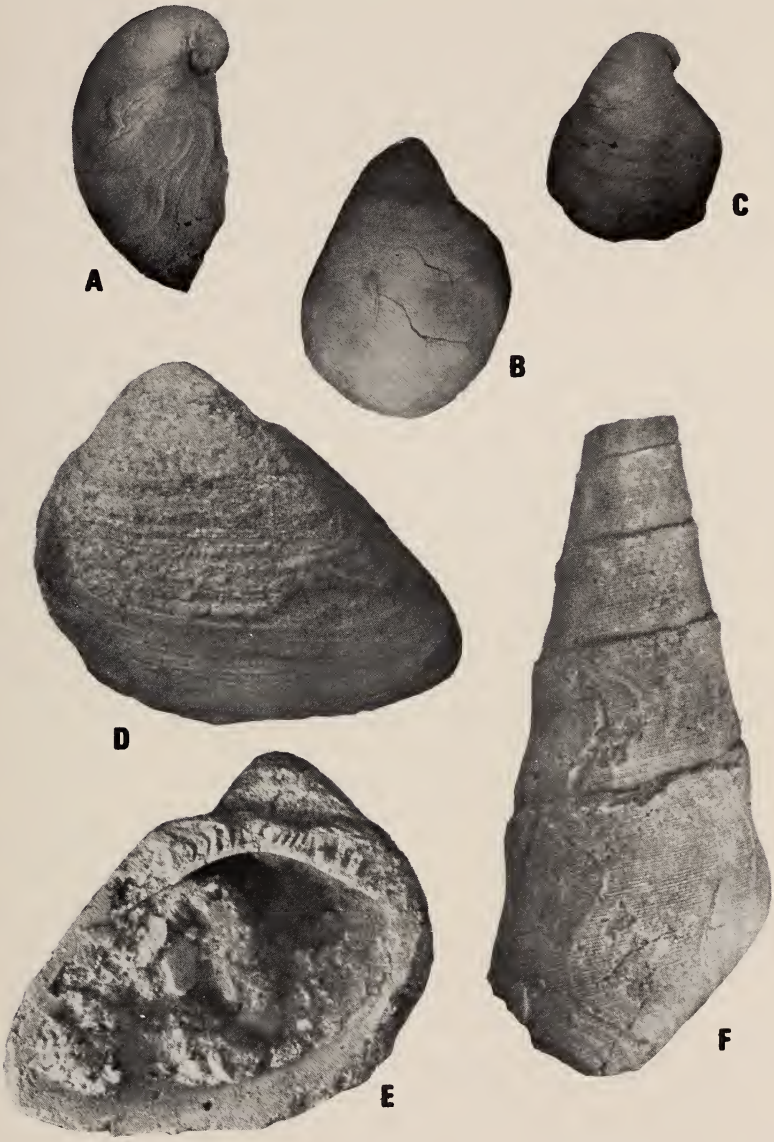

Fig. 3. A–C. *Rhynchostreon suborbiculatum* (Lamarck). D–E. *Trigonarca* sp. F. *Pseudomelamia salenasensis* Rennie. All specimens in the South African Museum collections. × 1.

Protocardia hillana (J. Sowerby) and *Veniella forbesiana* (Stoliczka), but are entirely lacking in ammonites. Three metres of unfossiliferous brownish limestones, weathering with a highly jagged surface, and interbedded silts separate this horizon from the first unit containing *Calycoceras naviculare* (Mantell). However, it is only 2,50 m higher up, in the lowest horizon of calcareous nodules that ammonites become relatively abundant. At this point the section becomes difficult to follow but there would appear to be, in all, some eight such nodular horizons in a thickness of about 6 m. These nodules are extremely hard and highly fossiliferous, being characterized by the abundance of the bivalve *Rhynchostreon suborbiculatum* (Lamarck).

SYSTEMATICS

All catalogue numbers refer to the collections housed in the South African Museum. Measurement abbreviations are as follows: D, diameter; H, whorl height; W, whorl width (intercostal unless otherwise specified); Ui, diameter of umbilicus between umbilical seams; Uo, diameter of umbilicus between umbilical bullae; W/H, whorl width/height ratio. All measurements are given in millimetres, and percentages follow in parentheses.

Class CEPHALOPODA Cuvier, 1797
Subclass AMMONOIDEA Zittel, 1884
Order LYTOCERATIDA Hyatt, 1899
Suborder LYTOCERATINA Hyatt, 1899
Superfamily TETRAGONITACEAE Hyatt, 1900
Family **Tetragonitidae** Hyatt, 1900
Genus *Tetragonites* Kossmat, 1895
Type species *Ammonites timotheanus* Pictet, 1847

1895 *Lytoceras* (*Tetragonites*) Kossmat
1925 *Epigoniceras* Spath
1935 *Saghalinites* Shimizu (nom. nud.)
1935 *Neoepigoniceras* Shimizu (nom. nud.)
1935 *Eoepigoniceras* Shimizu (nom. nud.)
1954 *Epigoniceras* (*Saghalinites*) Wright & Matsumoto

Discussion

Much attention has recently been paid to the Tetragonitidae (Wiedmann 1962, 1973; Murphy 1967*a*), and a relatively stable taxonomic classification appears to have been produced.

Wiedmann (1973: 588) rejected Murphy's (1967*a*) emphasis on constrictions as a basis for classification since 'number and course of constructions vary with age', consequently basing his taxa on whorl section and the persistence of conconstrictions. Sutural differences were regarded as of limited taxonomic use.

A number of workers (Howarth 1958: 9; Wiedmann 1962: 131, 171) have pointed out that *Epigoniceras* is indistinguishable from *Tetragonites*, while Wiedmann (1973: 589) does not regard the development of distinct umbilical

shoulders as an adequate basis for the generic separation of *Saghalinites*. The new genus *Carinites* Wiedmann was proposed for the keeled Cenomanian *T. spathi* (Fabre 1940: 214, pl. 6 (fig. 1), text-fig. 26), but appears to be of dubious status.

Tetragonites sp. nov.? aff. *blaisoni* Collignon, 1964

Figs 4P–Q, 5

Compare

Tetragonites blaisoni Collignon, 1964: 31, pl. 324 (fig. 1448). Wiedmann, 1973: 601, pl. 1 (fig. 4), pl. 6 (figs 5–7) text-fig. 7.

Tetragonites collignoni Murphy (*?non* Breistroffer), 1967*a*: 66, pl. 5 (figs 2–3), text-fig. 36a only.

Tetragonites subtimotheanus Murphy (*non* Wiedmann), 1967*a*: 62, pl. 6 (figs 5–8), ? text-fig. 35a–d only.

Description

The recrystallized test of the specimen has been preserved and is moderately involute, with about 75 per cent of the preceding whorl covered. The umbilicus is rather narrow (± 28% of diameter) and fairly deep, with broad, inclined umbilical walls and angular umbilical shoulders. The flanks are flat and converge noticeably towards the flat venter. The whorl section is depressed, trapezoidal, with the greatest width at the umbilical shoulder.

The ornament comprises weak, periodic, strongly prorsiradiate collars on the flanks, which cross the venter with a very slight concave-adoral arch.

Measurements

No.	D	H	W	W/H	Ui
SAM–PCA2818	31	13 (42)	16 (52)	1,23	9 (29)
,,	22	9 (41)	10 (45)	1,11	6 (27)

Discussion

The unique Angolan example is fragmentary, hence comparison with other members of the genus is difficult.

The relative proportions of the Salinas specimen are virtually identical to those of Kossmat's holotype of *T. subtimotheanus*, and easily fall within the range of morphometric variation shown by this species (Wiedmann 1973). The whorl section is also closely comparable, except that in *T. subtimotheanus* Wiedmann the umbilical wall is almost vertical, whereas in the Angolan example it is very distinctly inclined (Fig. 5). In the fragmentary Angolan specimen it is not possible to decide how many constrictions there were per whorl, but in general form they closely resemble those of *T. subtimotheanus*. In North America, *T. subtimotheanus* ranges from the upper Lower Albian (*hulenense* Zone) to the Lower Cenomanian, although elsewhere it appears to be confined to the Upper Albian. In view of the different stratigraphic ages and the slight but distinct

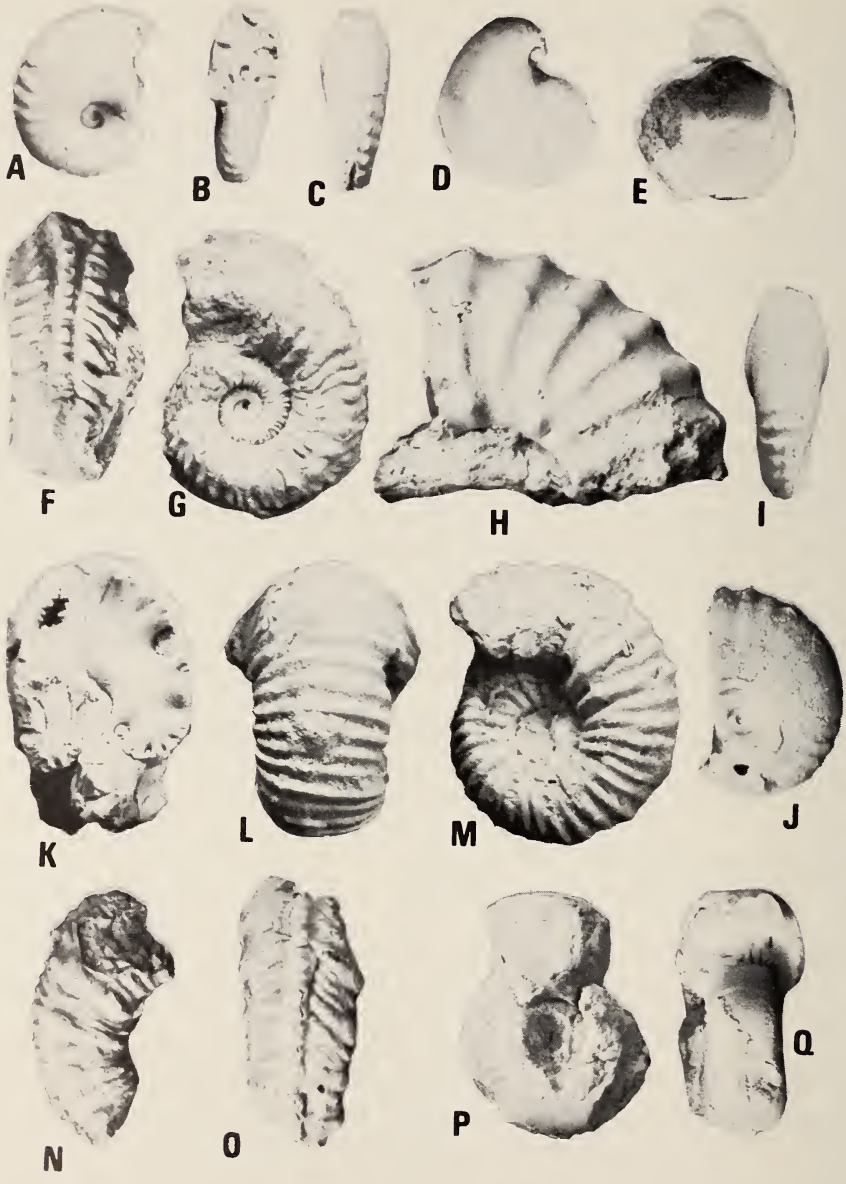

Fig. 4. A–C, H–K. *Pseudocalycoceras angolaense* (Spath). A–C. SAM–PCA2777. H–I. SAM–PCA2719. J–K. SAM–PCA2767. D–E. *Rhynchostreon suborbiculatum* (Lamarck), SAM–PCA2801. L–M. *Calycoceras* (*Calycoceras*) *naviculare* (Mantell), SAM–PCA2762. F–G, N–O. *Euomphaloceras* (*Kanabiceras*) *septemseriatum* (Cragin), SAM–K2878, K2779. P–Q. *Tetragonites* sp. nov. ? aff. *blaisoni* Collignon, SAM–PCA2818. × 1.

Fig. 5. *Tetragonites* sp. nov. ? aff. *blaisoni* Collignon. Whorl section of SAM–PCA2818. ×1.

difference in whorl-section, the Angolan example can only be regarded as a closely allied, but different, species.

Tetragonites rectangularis ampakabensis Collignon, from the Lower Cenomanian of Madagascar, differs in being more involute (U=20–23% of diameter), somewhat more depressed, and with steeper umbilical walls. *Tetragonites blaisoni* Collignon has similar relative proportions to the Salinas example, while the configuration of the constrictions is also closely comparable. It differs, however, in having much steeper umbilical walls and in being a Lower Cenomanian form.

According to the amended diagnosis of *Tetragonites glabrum* Jimbo given by Matsumoto (1942*b*: 671), this species has a small umbilicus (20–26% of diameter), with slightly depressed whorls. The flanks converge to a rounded venter, while constrictions are few and irregular in development.

Tetragonites epigonum (Kossmat) has an almost square whorl section (Usher 1952: 55), with not more than three prorsiradiate constrictions per whorl which appear to be effaced across the venter.

Tetragonites jurinianus (Pictet) lacks constrictions at all growth stages, while in *T. nautiloides* (Pictet) constrictions are present only at diameters of less than 10 mm.

The Angolan specimen is the only example of a *Tetragonites* yet recorded from uppermost Cenomanian strata, and in view of the slight, but distinct, differences from all previously recorded species of this genus, it probably merits a new specific name. The author hesitates to do so, however, due to the poor preservation of the unique Angolan example.

Family **Gaudryceratidae** Spath, 1927

Discussion

The family Gaudryceratidae has been subdivided into a number of subfamilies—Gaudryceratinae (Spath 1927), Gabbioceratinae (Breistroffer 1953), Kossmatellinae (Breistroffer 1953) and Vertebritinae (Wiedmann 1962). The usefulness and desirability of these groupings are questionable. *Vertebrites* is herein regarded as only a subgenus of *Gaudryceras* and consequently the Vertebritinae must fall into synonymy (cf. Henderson 1970: 22). Moreover, the close affinities of *Kossmatella* and *Anagaudryceras* are shown by the fact that the newly proposed species *Kossmatella* (*Murphyella*) *enigma* Matsumoto, Muramoto & Takahashi, type of the subgenus, is herein considered a junior subjective synonym of *Anagaudryceras buddha* (Forbes) (= *A. sacya* Forbes), thereby suggesting the superfluity of the subfamily Kossmatellinae.

The subfamily Gabbioceratinae Breistroffer was considered by Murphy

(1967*b*) to include only two genera, *Gabbioceras* and *Jauberticeras*, and characterized by a wide crater-like umbilicus, with flat, sloping umbilical walls, and a prominent ventro-lateral angulation of the whorls. Maximum width of the whorls was at this angulation. Ornament comprises fine, sinuous lirae and constrictions as in *Gaudryceras*. According to Murphy (1967*b*: 604), 'The principal difference between *Jauberticeras* and *Gabbioceras* is in the position of the angulation or, alternatively expressed, the relative curvature of the venter. In *Jauberticeras*, the angulation is very high and the curvature of the venter low; in *Gabbioceras*, the angulation is at about mid flank and the degree of curvature is high.' The differences are not herein considered of generic importance, and the Gabbioceratinae thus becomes a monogeneric subfamily of doubtful systematic value.

Genus *Gaudryceras* de Grossouvre, 1894

Type species *Ammonites mitis* Hauer, 1866

1894 *Gaudryceras* de Grossouvre
1926 *Vertebrites* Marshall
1934 *Epigaudryceras* Shimizu
1934 *Pseudogaudryceras* Shimizu
1934 *Hemigaudryceras* Shimizu
1935 *Neogaudryceras* Shimizu

Discussion

Wright (in Arkell *et al.* 1957: L200) considered the following features to be diagnostic of the genus *Gaudryceras*: 'Lirae coarser than in *Anagaudryceras*, close or distant, simple or branching, moderately to very sinuous; last whorl may bear variable close or distant strong foldlike ribs. Suture with retracted auxiliaries. May be divisible into subgenera but nominal groups cited in synonymy are not well differentiated.'

Wright & Matsumoto (1954) provided a detailed discussion of this genus, concluding that the genera *Epigaudryceras* (type species: *Ammonites crassicostatum* Jimbo), *Hemigaudryceras* (type species: *Ammonites denmanensis* Whiteaves), *Neogaudryceras* (type species: *Gaudryceras tenuiliratum* Yabe) and *Pseudogaudryceras* (type species: *Gaudryceras tenuiliratum* var. *infrequens* Yabe) were junior subjective synonyms of *Gaudryceras*.

Anagaudryceras Shimizu (type species: *Ammonites sacya* Forbes, 1846: 113, pl. 14 (fig. 10)) was regarded as a synonym of *Gaudryceras* by Wiedmann (1962: 156–158). As noted by Howarth (1965: 357), however, 'The ornament of all but the adult stage of *Anagaudryceras* is so fine that the shell appears to be smooth, while *Gaudryceras* is characteristically covered with fine ribs. This difference is sufficient for generic distinction in keeping with the scale of differences usually adopted for Cretaceous genera.'

Mesogaudryceras Spath (type species: *Ammonites leptonema* Sharpe, 1855: 32, pl. 14 (fig. 3)) differs from *Gaudryceras* in possessing compressed inner whorls, broad convex flanks, and a narrowly arched venter. It is also more involute than *Gaudryceras*.

Vertebrites Marshall (type species: *Vertebrites murdochi* Marshall, 1926: 139, pl. 20 (fig. 9), pl. 30 (figs 1–2), pl. 40 (fig. 2)) is an Upper Senonian–Maastrichtian genus, more evolute than *Gaudryceras* and retaining a flattened venter to larger growth stages, so that the ventro-lateral shoulders tend to become subangular. Fine flank lirae increase by bifurcation and intercalation across the venter. These ribbing characteristics are developed in a number of typical *Gaudryceras*, e.g. *Gaudryceras vertebratum* Kossmat, *Gaudryceras stefaninii* Venzo (W. J. Kennedy pers. comm.), and thus the only distinct difference between *Vertebrites* and *Gaudryceras* is that the former is more evolute and tends to become serpenticone, while the tabulate venter is retained to large diameters. The writer does not regard these differences as generic and prefers to treat *Vertebrites* as a subgenus of *Gaudryceras* (cf. Matsumoto 1959*b*: 141).

Eogaudryceras Spath (type species: *Ammonites numidus* Coquand in Sayn 1890: 144, pl. 1 (figs 3–4)) is a Lower Cretaceous genus, moderately evolute and with an initially trapezoidal whorl section becoming rounded with age. Ornament comprises fine, dense, slightly sinuous lirae and constrictions on the inner whorls only. It thus superficially resembles *Anagaudryceras*.

Gaudryceras (*Gaudryceras*) *isovokyense* Collignon, 1964

Figs 6A–B, 7

Gaudryceras isovokyense Collignon, 1964: 31, pl. 324 (fig. 1447).

Description

One well-preserved specimen, partially retaining recrystallized test, is assigned to this species.

The shell is entirely septate to a diameter of 74 mm. It is very evolute, with about 30 per cent of the preceding whorl covered. The whorl section at the adoral end of the outer whorl is oval, slightly depressed, with convex flanks converging slightly towards the evenly rounded venter. The preceding whorl, however, shows a more depressed whorl section with a broad, almost flat, venter (Fig. 7), as in the holotype. The umbilicus is wide and shallow, with a moderately steep umbilical wall and a well-rounded umbilical shoulder.

The ornament comprises fine, sharp lirae which begin at the umbilical seam, are slightly prorsiradiate on the umbilical wall, curve forward more strongly on the umbilical shoulder, sweep across the flanks and recurve so as to pass straight across the venter. At two places on the outer whorl, about 340° apart, 2–4 adjacent ribs are crowded together, thicker and slightly flared. This feature is associated only with the external shell as no constrictions are visible on the internal mould. Across the venter, the flank ribs become finer and increase by intercalation and bifurcation. Thus 19 flank ribs correspond to 28 ribs across the venter. On the anterior portion of the outer whorl there are 12 ribs within a 10 mm distance along the venter, whereas on the posterior position there are 16 in the same distance.

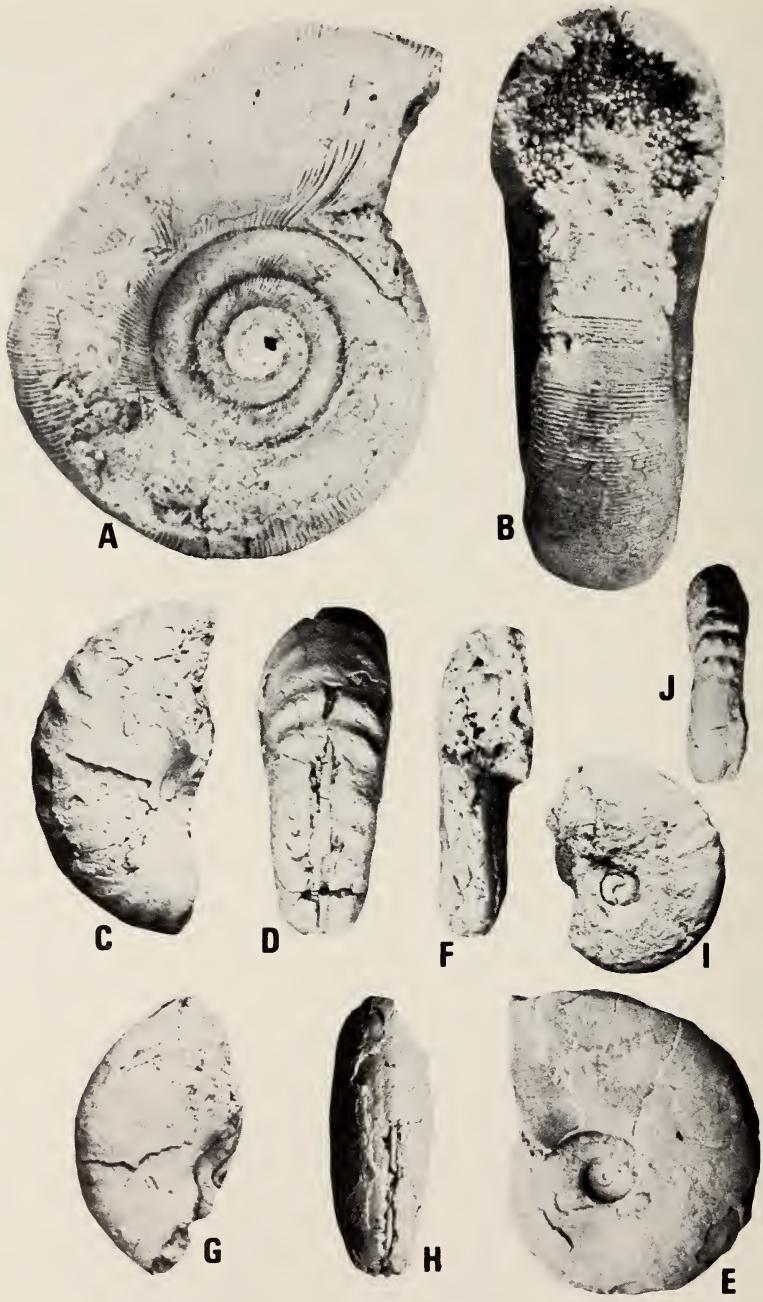

Fig. 6. A–B. *Gaudryceras* (*Gaudryceras*) *isovokyense* Collignon, SAM–PCA2713. C–H. *Vascoceras* (*Paravascoceras*) cf. *cauvini* Chudeau. C–D. SAM–PCA2816. E–F. SAM–PCA2727. G–H. SAM–PCA2796. I–J. *Pseudocalycoceras* sp., SAM–K2760. ×1.

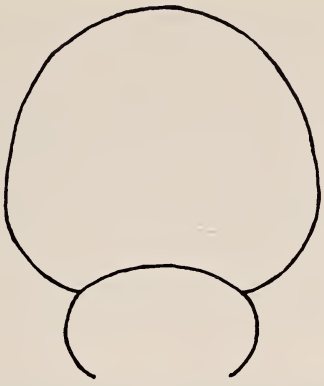

Fig. 7. *Gaudryceras* (*Gaudryceras*) *isovokyense* Collignon.
Whorl section of SAM–PCA2713. ×1.

Measurements

No.	D	H	W	W/H	Ui
SAM–PCA2713	74	25 (34)	28 (38)	1,12	29 (26)
,,	54	17 (31)	21 (39)	1,23	25 (22)
,,	37	11 (30)	17 (46)	1,55	21 (18)

Discussion

So far as can be judged, the penultimate whorl of the Salinas example is identical with the holotype of *G. isovokyense* from the Cenomanian 'Zone à *Mantelliceras mantelli* et *Calycoceras newboldi*' of Madagascar (Collignon 1964).

Gaudryceras varagurense Kossmat (1895: 122, pl. 17 (fig. 4), pl. 18 (figs 2a–c)), known from the Cenomanian to uppermost Campanian, differs from *G. isovokyense* in retaining an evenly rounded venter throughout ontogeny, having more frequent flared ribs and in that the rib density remains the same across the venter.

Gaudryceras stefaninii (Venzo) (1936: 21, pl. 2 (figs 3–4)) from the Cenomanian of Zululand bears a close resemblance to the Angolan material. This species differs, however, in having much finer, denser, *Vertebrites*-like ribbing across the venter.

Gaudryceras vertebratum Kossmat (1895: 126, pl. 15 (figs 4–5)) shows a flattened venter which is apparently 'smooth', with prorsiradiate lirae on the flanks.

Gaudryceras (*Vertebrites*) *murdochi* (Marshall) (Henderson 1970: 22, pl. 3 (fig. 1)) is an Upper Campanian species, very evolute, serpenticone with strongly depressed whorls and a broad flat venter.

Gaudryceras varicostatum (van Hoepen) (1921: 7, pl. 2 (figs 10–12)) shows dense fine lirae across the venter, but the latter is not nearly so flattened as in

G. isovokyense. Constrictions also appear to be more frequent in Van Hoepen's species.

Gaudryceras (*?Vertebrites*) *kayei* (Forbes) (1846: 101, pl. 8 (fig. 3)) is a very evolute, serpenticone form, with a broad, convex venter and about four constrictions on the outer whorl. The specimen figured by Stoliczka (1865: 156, pl. 77 (figs 1–2)) shows the same features as Forbes's example, but with a somewhat more flattened venter. The ornament comprises fine prorsiradiate flank ribs which, according to Stoliczka (1865: 156), 'bi-, or tri-furcate at the edge of the umbilicus (= ventro-lateral shoulder)'. This species differs from both *G. stefaninii* (Venzo) and *G. vertebratum* Kossmat in having a convex and not flattened venter.

Occurrence

This species is currently known only from Angola and Madagascar.

Genus *Anagaudryceras* Shimizu, 1934

Type species *Ammonites sacya* Forbes, 1846

1934 *Anagaudryceras* Shimizu
1934 *Paragaudryceras* Shimizu
1972 *Kossmatella* (*Murphyella*) Matsumoto, Muramoto & Takahashi

Discussion

Anagaudryceras is a long-ranging genus known from the Albian to the Maastrichtian. A host of species have been described but, as noted by Howarth (1965), the majority are nominal species, of little taxonomic value. Differences from *G.* (*Gaudryceras*) and *G.* (*Vertebrites*) are noted above.

The newly proposed subgenus *Kossmatella* (*Murphyella*) was diagnosed (Matsumoto *et al.* 1972: 208) as follows: 'The *Kossmatella* type ribs occur on relatively early inner whorls (with diameters from several millimetres to 10 or 15 mm), but on the late inner whorls the ribs and furrows are sparse and rather weak. In other words smoothish part is predominant over the ribbed or constricted part in the middle growth stage. In the late septate whorl and the adult body-whorl the fold ribs and intervening furrows are distinct.'

Thus, *Murphyella* supposedly differs from the contemporaneous *Anagaudryceras* only in possessing fold-like ribs and constrictions at a very early stage in growth, although, as noted by Matsumoto *et al.* (1972), these are variable in persistence and intensity. However, McLearn (1972) has recently shown identical features to occur in *Anagaudryceras sacya* (= *A. buddha*), and the author has little hesitation in regarding *Kossmatella* (*Murphyella*) as a junior subjective synonym of *Anagaudryceras*.

Anagaudryceras cf. *cassisianum* (d'Orbigny, 1850)
Figs 8–9, 10J, 11B–D

Compare

Ammonites cassisianus d'Orbigny, 1850: 146.
Ammonites madraspatanum Stoliczka, 1865: 151, pl. 75 (fig. 2).
Anagaudryceras madraspatanum (Stoliczka) Matsumoto, 1959*a*: 74, pl. 22 (fig. 3).
Gaudryceras salinarium Douvillé, 1931: 42, pl. 1 (fig. 3), text-fig. 5.

Description

Two examples, one a juvenile and the other a fragment of an adult, both with recrystallized test preserved, are close to d'Orbigny's species.

Fig. 8. *Anagaudryceras cassisianum* (d'Orbigny). D'Orbigny's syntypes from the Cenomanian of Cassis, France. Photo: W. J. Kennedy. ×1.

The juvenile example, SAM–PCA2769 (Fig. 11B–D), is very evolute (umbilicus 46–50% of diameter), with about one-sixth of the preceding whorl covered. The umbilicus is wide and shallow, with a steep umbilical wall and a well-rounded umbilical shoulder. The flanks are strongly convex and converge towards the evenly rounded venter.

The ornament comprises extremely fine, indistinct, flexuous lirae which arise at the umbilical seam, pass forward across the umbilical wall, swing forward more strongly on the flanks, then recurve gently so as to cross the venter transversely. There appear to be occasional, very weak constrictions on the earliest whorls.

SAM–PCA2726 (Fig. 10J) is a fragment of a mature individual. The whorl section is unknown. Ornament comprises fine lirae which arise at the umbilical seam and pass forward (prorsiradiate) to the umbilical shoulder where they increase by bifurcation and intercalation. The lirae are almost rectiradiate across the flank. A prominent collar, following much the same course as the lirae, splits into three fine ribs across the flanks. Although a much larger diameter, this specimen very closely resembles d'Orbigny's larger syntype of *Ammonites cassisianus*.

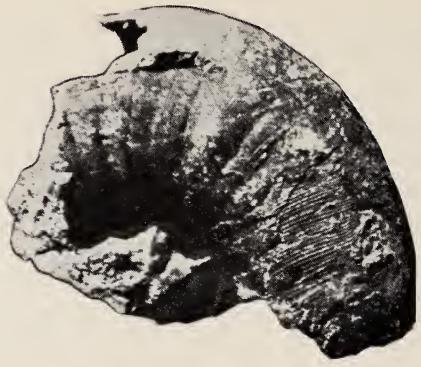

Fig. 9. *Anagaudryceras* cf. *cassisianum* (d'Orbigny). The holotype of *Gaudryceras salinarium* Douvillé (after Douvillé 1931). ×1.

Measurements

No.	D	H	W	W/H	Ui
SAM–PCA2769	39	15 (38)	18 (46)	1,20	?
,,	28	8 (29)	12 (43)	1,50	13 (46,4)
,,	22	6 (27)	10 (45)	1,70	11 (50)

Discussion

D'Orbigny's syntypes (Fig. 8) show the following features: the shell is evolute (umbilicus 41–45% of diameter), with a wide, shallow umbilicus, evenly rounded umbilical shoulder, slightly convex flanks, and a rounded venter. The whorl section is almost circular, about as wide as high. On the inner whorls, extremely fine lirae arise at the umbilical seam and pass forward (prorsiradiate) to the umbilical shoulder where they increase by bifurcation and intercalation. On the flanks the lirae are initially prorsiradiate, but quickly recurve so as to become rectiradiate or slightly rursiradiate on the ventral half of the flanks. There are periodic collars which follow much the same course as the constrictions. On the outer whorls, the lirae become coarser and *Gaudryceras*-like, narrower than the interspaces, while collars split into coarse lirae on the flanks.

Gaudryceras salinarium Douvillé is based upon a fragmentary specimen with a circular whorl section, and showing broad *Anagaudryceras*-like flank ribs on which are superimposed *Gaudryceras*-like lirae (Fig. 9). Thus, the holotype of *G. salinarium* appears to differ from *A. cassisianum* only in what appear to be the broad flank ribs typical of mature *Anagaudryceras*. Of the new material from the Salinas locality, a large fragment (Fig. 10J) appears indistinguishable from d'Orbigny's species, but lacks the broad flank ribs of *G. salinarium*, while the juvenile (Fig. 11B–D) differs in possessing a depressed whorl section and very indistinct collars. Neither d'Orbigny's nor Douvillé's species are well known and the differences are well within the range of intraspecific variation observed in

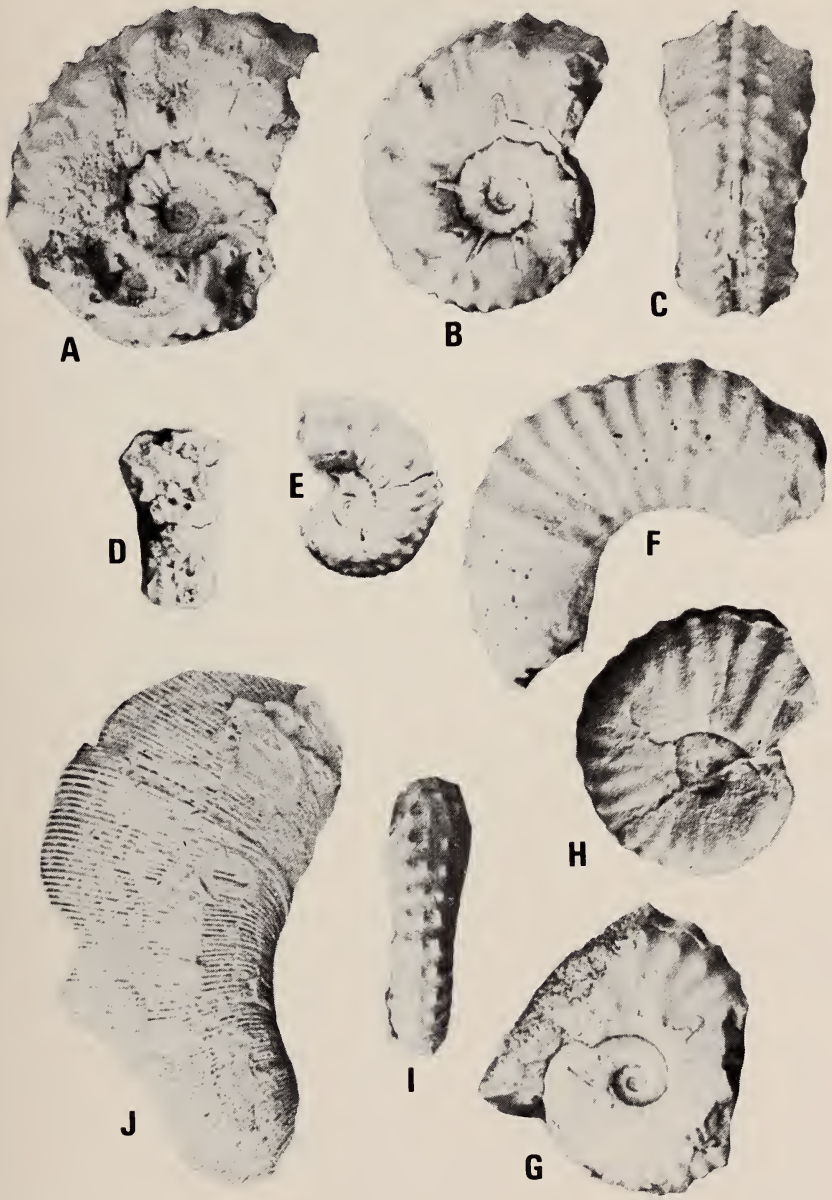

Fig. 10. A–E. *Euomphaloceras* (*Kanabiceras*) *septemseriatum* (Cragin). A. SAM–PCA2738. B–C. SAM–PCA2797. D–E. SAM–PCA2832. F–G. *Pseudocalycoceras angolaense* (Spath). F. SAM–PCA2743. G. SAM–PCA2772. H–I. *Pseudocalycoceras* aff. *haugi* (Pervinquière), SAM–PCA2775. J. *Anagaudryceras* cf. *cassisianum* (d'Orbigny), SAM–PCA2726. × 1.

many Cretaceous ammonite species. However, without additional material the problem cannot be resolved in this paper, and the Angolan material is referred to *Anagaudryceras* cf. *cassisianum* (d'Orbigny).

Other broadly contemporaneous species of *Anagaudryceras* include *A. buddha* (Forbes), *A. sacya* (Forbes), *A. involvulum* (Stoliczka), *A. revelatum* (Stoliczka), *A. madraspatanum* (Stoliczka), *A. utaturense* Shimizu, *A. multiplexus* (Stoliczka), *A. limatum* (Yabe), *A. aurarium* (Anderson) and *A. enigmum* (Matsumoto, Muramoto & Takahashi).

Since 1865, many workers (Stoliczka 1865, Kossmat 1895, Matsumoto 1959*a*) have realized that *Ammonites sacya* Forbes (1846: 113, pl. 14 (fig. 10)), the type of the genus *Anagaudryceras*, was merely based upon the inner whorls of *Ammonites buddha* Forbes (1846: 112, pl. 14 (fig. 9)), a body chamber fragment. Since *A. buddha* clearly has priority, it includes among its synonyms (cf. Howarth 1965) *A. sacya* (Forbes), *A. revelatum* (Stoliczka), *A. limatum* (Yabe) and *A. enigmum* (Matsumoto, Muramoto & Takahashi). *Anagaudryceras buddha* (Forbes) differs from *A. cassisianum* in maintaining extremely fine liration to maturity.

Anagaudryceras multiplexum (Stoliczka 1865: 151, pl. 75 (fig. 2)) differs from *A. cassisianum* in being somewhat more evolute (umbilicus 50% of diameter), with a steeper umbilical wall and more abrupt umbilical shoulder, as well as in retaining extremely fine liration to maturity.

Anagaudryceras madraspatanum (Blanford) (Stoliczka 1865: 151, pl. 75 (fig. 2)) was considered to show the following features: 'Shell consisting of numerous round whorls, which are only slightly involute, increasing regularly in height and thickness, and crossed by dense fine flexuous striae. On the casts of some of our specimens, slight transverse furrows are seen. . . . Umbilicus large and deep, three-fifths of the inner whorls being exposed; aperture circular.'

Matsumoto (1959*a*: 74, pl. 22 (fig. 3)) recorded *A. madraspatanum* from the Chitina Valley of Alaska and considered the diagnostic features to be 'the circular cross section of the whorl, little involution, fairly wide umbilicus, fine and dense striae and lirae on the surface of the shell that curve gently forward near the umbilical margin, but are nearly rectiradiate on the main part of the whorl, and the faint constrictions'. Of these characters, the prominence of constricted collars and the shape of the whorl section are known to vary with ontogeny, while the width of the umbilicus and the degree of involution of the shell are comparable with *A. cassisianum*. Adult specimens of *A. madraspatanum* are unknown and consequently the writer regards Stoliczka's (1865) species as a junior subjective synonym of *A. cassisianum*.

Anagaudryceras involvulum (Stoliczka) (1865: 150, pl. 75 (fig. 1)) is a compressed species with rapidly expanding whorls and about five constrictions on the outer whorl at 44 m diameter. This species has recently (Howarth 1968) been recorded from the Turonian of Ponta Grossa, Angola. It would seem to differ from *A. cassisianum* in being more compressed, and in not developing *Gaudryceras*-type lirae in maturity.

Fig. 11. A. *Puzosia* (*Anapuzosia*) *dibleyi* (Spath), SAM–PCA2792. B–D. *Anagaudryceras* cf. *cassisianum* (d'Orbigny), SAM–PCA2769. ×1.

Occurrence

Anagaudryceras cassisianum is at present recorded from France, Alaska, southern India and possibly Angola.

Suborder ANCYLOCERATINA Wiedmann, 1966
Superfamily ANCYLOCERATACEAE Meek, 1876
Family **Baculitidae** Meek, 1876
Subfamily Baculitinae Meek, 1876
Genus *Sciponoceras* Hyatt, 1894
Type species *Hamites baculoide* Mantell, 1822

Sciponoceras gracile (Shumard, 1861)

Fig. 12B–D

Baculites gracilis Shumard, 1861: 596. Stanton, 1893: 1166, pl. 34 (figs 1–3). Grabau & Shimer, 1910: 179, fig. 1432. Adkins, 1928: 206, pl. 24 (fig. 3). Moreman, 1942: 210.
Baculites ovatus White (*non* Say), 1876: 199, pl. 19 (figs 4–5).
Sciponoceras gracile (Shumard) Cobban, 1951: 2185. Matsumoto, 1959*b*: 106. Matsumoto & Obata, 1963: 23. Cobban, 1955: 202, pl. 2 (fig. 3). Cobban & Scott, 1972: 47, pl. 17 (figs 9–29). Wright & Kennedy, 1973 (in Juignet *et al.* 1973): 21, pl. 1 (figs 2–6).
Baculites n. sp. aff. *bohemicum* Fritsch, Kossmat, 1895: 154, pl. 19 (fig. 18).
Baculites kossmati Nowak, 1908: 348.
Baculites cfr. *gaudini* Pictet & Campiche, Matsumoto, 1942*a*: 229.
Sciponoceras kossmati (Nowak) Matsumoto, 1959*b*: 106, pl. 31 (figs 2–3). Matsumoto & Obata, 1963: 13, pl. 3 (fig. 2), pl. 4 (fig. 1), pl. 5 (figs 1–3), pl. 6 (figs 3–5).
Cyrtochilus stylus Anderson, 1958: 188, pl. 11 (fig. 5).

Description

A single fragment, with the recrystallized test preserved, is the only specimen assignable to this genus from Salinas.

The shell tapers slowly adapically and has a very compressed, elliptical whorl section, with flattened sides. The ornament, which is very faint, comprises weak, prorsiradiate constrictions, most prominent across the venter but becoming effaced across the lower flanks and dorsum, and very faint ribs which follow the course of the constrictions. There would appear to be one, possibly two, such constrictions within a distance equal to the major diameter. At a major diameter of 9 mm the width is only 6 mm.

Discussion

Shumard (1861: 596) described *Sciponoceras gracile* as follows: 'Shell very slender, gradually tapering to apex; transverse section varying from broad ovate to subcircular; surface in some specimens nearly smooth, but usually marked with moderately prominent, rounded costae, which on the dorsum (venter) are distinct and arched towards the aperture, and on the sides curve obliquely backwards and downwards to the ventral margin (dorsum), before reaching which they become nearly obsolete. Some of the specimens exhibit very fine flexuous striae of growth.'

Shumard's type material has never been figured or adequately redescribed, nor has a lectotype been designated. According to Wright & Kennedy (in Juignet *et al.* 1973: 21) the type material is probably in the University of Texas collections.

Wright & Kennedy (in Juignet *et al.* 1973: 21) have recently discussed this species on the basis of topotype material from the *Sciponoceras gracile/Metoiceras whitei* Zone (Cobban 1951) of the Gulf Coast and Western Interior of North America, and material from the late Cenomanian of southern England and northern France. These authors show this species to be characterized by a compressed, elliptical whorl section with flattened sides and broad prorsiradiate constrictions spaced at intervals slightly greater than the major diameter. Between constrictions there are 5–6 ribs. Both ribbing and constrictions are most prominent across the venter, becoming obsolete before the dorsum is reached. Shumard's (1861) descriptions leave little doubt that there is a fair degree of variability in the prominence of the ornament of this species, and consequently the weak ornament of the Angolan example is not considered significant.

Sciponoceras roto Cieslinski differs in having an almost circular whorl section at all growth stages, while *S. baculoide* (Mantell) has more distant constrictions (one every 1,5–2 major diameters), a less compressed whorl section, and coarser, more robust ventral ribbing (on the body chamber at least).

Sciponoceras glaessneri Wright (1963: 599, pl. 81 (figs 2–3)) from the Middle Cenomanian of Bathurst Island, Australia, is more inflated at large growth stages, with more convex flanks, and lacks distinct ventral ribbing.

Sciponoceras kossmati (Nowak) (= *Baculites* sp. nov. aff. *bohemicum* Fritsch, Kossmat, 1895: 154, pl. 19 (fig. 18)) is the most important synonym of *S. gracile*. *Sciponoceras kossmati* was said (Matsumoto 1959*b*: 107) to have 'narrower and more deeply incised saddles . . . while the external saddle is much broader than the lateral saddle in *S. gracile*, the former is nearly as broad as and somewhat lower than the latter in *S. kossmati*. The general outline of the sutural elements is reversed trapezoidal in *S. kossmati*, but is rectangular in *S. gracile*.' However, not only are they morphologically indistinguishable (Matsumoto & Obata 1963), but they also occur at the same stratigraphical horizon. Moreover, Matsumoto & Obata (1963) have noted considerable variation in the suture of *S. kossmati*. In Japan, *S. kossmati* is associated with *Calycoceras naviculare* (Mantell), *Euomphaloceras* (*Kanabiceras*) *septemseriatum* (Cragin), *Tarrantoceras faustum* (Matsumoto & Muramoto) and *Pseudocalycoceras angolaense* (Spath). These are typical uppermost Cenomanian forms and the author regards *S. kossmati* as a junior subjective synonym of *S. gracile*.

Occurrence

This species is recorded from the top Cenomanian of California, the Western Interior, Texas, England, France, and Angola, and the uppermost Cenomanian–?basal Turonian of India and Japan.

Fig. 12. A. *Calycoceras* (*Calycoceras*) *naviculare* (Mantell), SAM–PCA2764. B–D. *Sciponoceras gracile* (Shumard), SAM–PCA2724. E–H. *Euomphaloceras* (*Kanabiceras*) *septemseriatum* (Cragin). E–F. SAM–PCA2761. G–H. SAM–PCA2835. × 1.

Superfamily HOPLITACEAE Douvillé, 1890
Family **Desmoceratidae** Zittel, 1895
Subfamily Puzosiinae Spath, 1922
Genus *Puzosia* Bayle, 1878
Type species *Ammonites planulatus* J. de C. Sowerby, 1827

1878 *Puzosia* Bayle
1900 *Pleuropachydiscus* Hyatt
1922 *Austiniceras* Spath
1954*a* *Anapuzosia* Matsumoto
1954*a* *Mesopuzosia* Matsumoto

Discussion

Since the inception of Bayle's genus *Puzosia* in 1878, a host of names have been proposed for closely allied forms.

The genus *Mesopuzosia* Matsumoto (type species *Mesopuzosia pacifica* Matsumoto, 1954*a*: 82, pl. 14 (fig. 1), pl. 15 (figs 1–2), pl. 16 (figs 1–3)) was said (Matsumoto 1954*a*: 79) to be 'similar to *Puzosia* in shell form and suture-line but with much better developed costae. In the middle and adult stages of growth many of the costae (including both longer and some shorter ones) extend below the middle of the flanks and are of equal strength on the outer half of the whorls. Although there are longer and shorter ribs, the differentiation to broader (or stronger) and narrower ones is not found as in *Parapuzosia* (s.s.) or in *Austiniceras* and the costation is relatively regular. The shell often attains a huge size and in the last whorl the ornamentation disappears.'

Wiedmann & Dieni (1968) considered *Mesopuzosia* to be a 'stratigraphische Gattung' and placed it in synonymy with *Puzosia* s.s. However, the differences between the types of *Mesopuzosia* and *Puzosia* are at least as great as between the latter genus and *Austiniceras*. Consequently, the writer prefers to retain *Mesopuzosia* as a subgenus of *Puzosia*.

Anapuzosia Matsumoto (type species *Puzosia buenaventura* Anderson, 1938: 185, pl. 40 (fig. 3), pl. 41 (figs 1–2)) was erected as a subgenus of *Puzosia*, and separated from *Puzosia* s.s. on body chamber characteristics. In *Puzosia* s.s., ribbing remains consistently fine to the aperture, whereas in *Anapuzosia* the 'adult body chamber is ornamented with periodic, flared or tuberculated, strong ribs of little or no flexuosity' (Matsumoto 1954*a*: 71). According to the emended diagnosis of Renz (1972: 704), in *Anapuzosia* ribs arise at the umbilical shoulder, are flexuous and either bifurcate or are joined by intercalatories across the venter. In some cases, there may be up to three intercalatories between main ribs. These differences are in keeping with the other generic and subgeneric separations within the Puzosiinae, and consequently the writer follows Renz (1972) in regarding *Anapuzosia* as a valid subgenus of *Puzosia*. The writer is not inclined to attach much weight to the change in ornament on the body chamber since, where sexual dimorphism in ammonites has been proved, the macroconch (female) dimorph commonly shows a marked change of ornament on the body chamber.

The genus *Austiniceras* Spath (type species *Ammonites austeni* Sharpe, 1855: 28, pl. 12 (fig. 1a–b only)) was diagnosed by Kennedy (1971: 37) as follows: 'Medium-sized to large puzosiids with a compressed, convergent whorl section and a narrowly arched venter. Moderately evolute, with 2 distinct orders or ribbing; distant, long flexuous main ribs with many shorter, flexuous intercalated ribs.'

The lectotype of *Austiniceras austeni* is a gigantic specimen 410 mm in diameter and juveniles of this species are not yet known. In southern England (Kennedy 1971), *A. austeni* ranges from low in the *mantelli* Zone to at least the Middle Turonian, and is one of the commonest Upper Cenomanian–Lower Turonian ammonites in this area. It is clearly obvious from Kennedy's (1971) excellent figure of the holotype that the inner whorls of this species cannot satisfactorily be distinguished from *Puzosia*. Moreover, there are a number of described *Puzosia* species from the Upper Cenomanian and Turonian which probably represent nothing more than the inner whorls of Sharpe's species. In Japan and California they are known as *Puzosia orientale* Matsumoto, in Madagascar as *P. orientale* and *P. praecompressa* Collignon, in Portugal as *P.* cf. *gaudama* (Forbes), and in India as *P. intermedia* Kossmat. It is clear, therefore, that *Austiniceras* is distinguished from some *Puzosia* species only by its large size and, where present, the change in ornament on the body chamber.

Within the genus *Puzosia* s.s., Wiedmann & Dieni (1968) recognized two species groups. The species group of *Puzosia quenstedti* (Parona & Bonarelli) was characterized by a moderately wide umbilicus (umbilical ratio 25–33%), flattened sides which converge towards the narrowly rounded venter and 6–7 constrictions per whorl. The constrictions are strong, radial, and with a strong convex ventral sinus. Species are separated on whorl section differences.

The species group of *Puzosia mayoriana* (d'Orbigny) was characterized by a relatively wide umbilicus (31–40% of the diameter), flattish, subparallel flanks and a broadly rounded venter. There are 4–6 rather deep, sigmoidal constrictions per whorl which form a chevron across the venter. These are the characters of *P. planulata* Sowerby (= *P. subplanulata* Schlüter), the type of the genus.

The genus *Puzosia* may now be subdivided as follows:

P. (*Puzosia*). Shell compressed, moderately evolute with 4–7 sinuous collars (constrictions on the internal mould) per whorl. Flanks flattish, subparallel, with a broadly rounded venter. Ribbing simple, distinct only on outer half of whorls. Age: Lower Albian–Upper Turonian.

P. (*Anapuzosia*). Similar to *P.* (*Puzosia*), but with ribs arising from near the umbilical shoulder and increasing by intercalation and bifurcation above mid-flank. All ribs and constrictions flexuous. Age: Lower Albian–Upper Cenomanian.

P. (*Austiniceras*). Similar to *P.* (*Puzosia*) but large, with flat convergent flanks and a narrowly arched venter. Generally straight, rigid constrictions, strongly projected on the venter. May attain large size, when body chamber

ornamented with close, dense, robust long ribs extending to the umbilical margin. Age: ? Albian–? Campanian, mainly Cenomanian–Turonian.

P. (*Mesopuzosia*). Similar to *P.* (*Puzosia*), but with straight, rigid constrictions, while ribbing may arise close to the umbilical shoulder. Age: Turonian–Coniacian.

Subgenus *Austiniceras* Spath, 1922
Type species *Ammonites austeni* Sharpe, 1855

Puzosia (*Austiniceras*) *intermedia orientalis* Matsumoto, 1959

Ammonites planulatus Stoliczka (*non* J. de C. Sowerby), 1865: 134, pl. 67 (figs 1a–b only).
Puzosia gaudama Kossmat (*non* Forbes), 1898: 118, pl. 16 (figs 2–3), pl. 22 (fig. 2).
Puzosia cf. *gaudama* (Forbes) Choffat, 1898: 82, pl. 17 (fig. 2), pl. 18 (fig. 1).
Puzosia orientale Matsumoto, 1954*a*: 74, pl. 13 (figs 1–2). Collignon, 1961: 32, pl. 5 (fig. 1).
Puzosia orientale kossmati Matsumoto, 1954*a*: 75.
Puzosia praecompressa Collignon, 1964: 55, pl. 332 (fig. 1493).
Puzosia intermedia orientalis Matsumoto, 1959*b*: 16, pl. 4 (fig. 1).

Diagnosis

A moderately evolute (umbilicus 27–34% of diameter), compressed (W/H = 0,70–0,78) species of *Puzosia* with about 4–6 straight, prorsiradiate constrictions which project strongly forward on the venter. Numerous fine, strongly prorsiradiate ribs intercalated on outer one-third of flanks between constrictions and projected strongly across the venter.

Description

The single specimen from these beds has the recrystallized test preserved. It is strongly compressed and moderately involute, with slightly more than half the preceding whorl covered. The umbilicus is fairly narrow and rather shallow, with a steep, slightly undercut umbilical wall.

The broad flanks are flat, converging slightly to the narrowly arched venter. The ornament comprises probably 4–5 straight prorsiradiate constrictions per whorl which project strongly forward across the venter. Between the constrictions are about 22 fine ribs which are present only on the outer one-third of the flanks.

Fig. 13. *Puzosia* (*Austiniceras*) *intermedia orientalis* Matsumoto, SAM–PCA2824. ×1.

Measurements

No.	D	H	W	W/H	Ui
P. orientale (holotype) .	126,3	50,0 (40)	38,7 (31)	0,78	43,3 (34)
Kossmat, 1898: pl. 22 (fig. 2) . . .	80,0	32,0 (40)	23,0 (29)	0,72	26,0 (32)
Choffat 1898: pl. 17 (fig. 2), pl. 18 (fig. 1) . .	125,0	57,0 (46)	40,0 (32)	0,70	34,0 (27)
P. praecompressa (holotype) . .	67,0	27,0 (40)	21,0 (31)	0,78	17,0 (25)
SAM–PCA2824 . .	40,0	17,0 (42)	12,0 (30)	0,70	12,0 (30)
,, . .	30,0	13,0 (43)	10,0 (33)	0,77	8,0 (27)

Discussion

The Angolan example clearly belongs to Wiedmann & Dieni's (1968) group of *Puzosia quenstedti*. It differs from the Upper Albian–Lower Cenomanian *Puzosia communis* Spath (1923: 47, pl. 2 (fig. 3a–e)) in possessing fewer constrictions per whorl.

Puzosia orientale orientale Matsumoto (1954*a*: 74, pl. 13 (figs 1–2)) was proposed for 'a species of *Puzosia* characterized by relatively compressed whorls, narrowly arched venter, numerous, regular, fine and narrow costae on the external half and the prorsiradiate course on sides and conspicuous forward bend on the periphery of the costae and the constrictions'.

Matsumoto's holotype, from the Lower Turonian of Japan, is poorly preserved, but judging from his description, his rather poor figures and the measurements, the Angolan example appears to be conspecific.

Puzosia orientale kossmati Matsumoto (= *P. gaudama* Kossmat (*non* Forbes), 1898: 118, pl. 16 (figs 2–3)) differs only in being slightly more evolute.

Puzosia muelleri Grossouvre (= *Ammonites hernensis* Schlüter, 1871: 40, pl. 9 (figs 12a–b, 14) (*non* Schlüter 1867)) is very similar to the Angolan specimen, differing only in being more compressed (W/H = 0,65) (? crushed). It is thus possibly conspecific with *P. compressa* Kossmat.

Puzosia subcorbarica Matsumoto (1954*a*: 73, pl. 9 (fig. 1), pl. 12 (fig. 1)) is a compressed form from the Upper Albian of Japan which is more compressed (W/H = 0,51—0,69) than *P. orientale*, with (?) slightly sigmoidal constrictions.

The Lower Cenomanian *Puzosia takei* Popovici-Hatzeg (1899: 12, pl. 2 (fig. 2)) is very similar to *P. orientale*, but is somewhat more evolute, with more constrictions.

Puzosia praecompressa Collignon (1964) is a junior subjective synonym of *P. intermedia orientalis*, as is clearly shown by Collignon's figure, description and measurements.

It is very doubtful whether *P. intermedia orientalis* can be distinguished from the inner whorls of the contemporaneous *Puzosia* (*Austiniceras*) *austeni* (Sharpe),

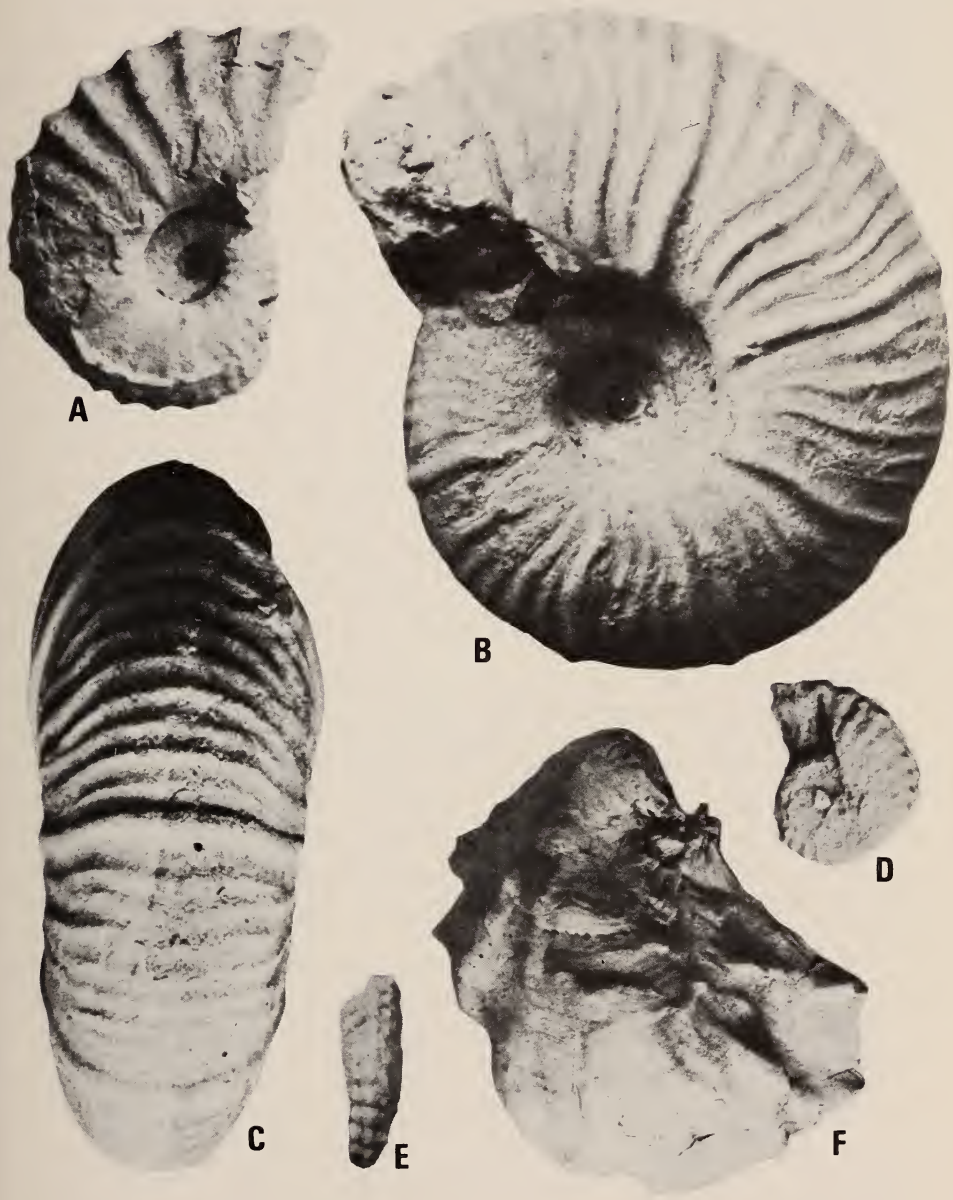

Fig. 14. A. *Pseudocalycoceras angolaense* (Spath), SAM–PCA2732. B–C. *Puzosia* (*Anapuzosia*) *dibleyi* (Spath), SAM–PCA2749. D–E. ?*Protacanthoceras* sp., SAM–PCA2804. F. *Exogyra* (*Costagyra*) *olisiponensis* Sharpe, SAM–PCA2752. ×1.

a species based solely on gigantic mature individuals. However, since the inner whorls of Sharpe's species are still unknown, the sinking of Matsumoto's species must await knowledge of the ontogenetic variation in *P.* (*A.*) *austeni.*

Occurrence

Puzosia intermedia orientale ranges from the Upper Cenomanian into the Lower Coniacian, and is known from Japan, India, Portugal, California, Madagascar and Angola.

Subgenus *Anapuzosia* Matsumoto, 1954
Type species *Puzosia buenaventura* Anderson, 1938

Puzosia (*Anapuzosia*) *dibleyi* (Spath, 1922)

Figs 11A, 14B–C, 15B–C

Ammonites austeni Sharpe, 1855: 28, pl. 12 (fig. 2 only).
Austiniceras dibleyi Spath, 1922: 127. Wright & Wright, 1951: 19. Kennedy, 1971: 39, pl. 13 (figs 1–2), pl. 14 (fig. 4).
Puzosia (*Austiniceras*?) *dibleyi* (Spath) Spath, 1931: 316.
Puzosia matheroni Douvillé (*non* d'Orbigny), 1931: pl. 2 (figs 5a–b).

Diagnosis

A medium-sized rather coarsely ribbed *Anapuzosia*, with 8–9 flexuous main ribs per whorl, between which are 5–9 coarse flexuous intercalatories, some of which arise close to the umbilical shoulder.

Description

This species is a common member of the Salinas fauna and, like most of the fossils from these beds, almost invariably has the recrystallized test preserved.

The shell is compressed to slightly depressed (W/H = 0,83–1,06), and moderately involute (umbilicus 27–32% of diameter), with about 65 per cent of the preceding whorl covered. The umbilicus is fairly narrow and moderately deep, with steep umbilical walls and an evenly rounded shoulder. The flanks are convex and converge towards the evenly arched venter. The whorl section is about as wide as high.

There are 8–9 prominent sinuous main ribs per whorl, between which are 5–9 flexuous intercalatories, a number of which arise near the umbilical shoulder whilst the remainder are only intercalated on the outer one-third of the flanks.

Measurements

No.	D	H	W	W/H	Ui
SAM–PCA2792	165	71 (43)	74 (45)	1,04	49 (30)
,,	103	44 (43)	45 (44)	1,02	33 (32)
SAM–PCA 2749	90	37 (41)	39 (43)	1,06	25 (27,7)
,,	70	30 (43)	29 (41)	0,97	20 (28,5)
SAM–PCA2748	97	40 (41)	41 (42)	1,03	30 (30,9)
,,	75	32 (43)	31 (41)	0,97	22 (30)
,,	27	12 (44)	10 (37)	0,83	?

Discussion

Puzosia (*Anapuzosia*) *dibleyi* has long been referred to *Austiniceras*. At present, this species is known only from north-western Europe and Angola. The British material is based upon crushed composite internal moulds, whereas the well-preserved Angolan material has the recrystallized test preserved and is thus more valuable in determining the generic status of this species.

As already pointed out, the differences between *Austiniceras* and *Puzosia* s.s. are slight, and the author prefers to treat the former as a subgenus of the latter. *Austiniceras austeni* differs from *Puzosia subplanulata* (Schlüter) in its flat converging flanks, narrowly arched venter, generally rigid constrictions and its large size. *Puzosia dibleyi* (Spath) differs from *P.* (*Austiniceras*) *austeni* in its smaller size, flexuous main ribs, convex flanks, evenly arched venter, and in that many of the intercalated ribs arise close to the umbilical shoulder. These are the exact features which are herein considered to be diagnostic of *Anapuzosia* and the author therefore has no hesitation in referring Spath's species to this subgenus.

The Albian species *P.* (*Anapuzosia*) *saintoursi* Collignon (1963*b*: 61, pl. 263 (fig. 1150), 68, pl. 266 (fig. 1157)), *P.* (*A.*) *colusaensis* (Anderson) (1902: 96, pl. 5 (figs 128–129), pl. 10 (fig. 200)), *P.* (*A.*) *multicostata* Renz (1972: 707, pl. 2 (figs 1–2), pl. 3 (fig. 1), pl. 9 (fig. 4)) all have finer, more numerous intercalatories.

Occurrence

This species is known only from southern England and Angola.

Subfamily Desmoceratinae Zittel, 1895
Genus *Desmoceras* Zittel, 1884
Type species *Ammonites latidorsatus* Michelin, 1836

1884 *Desmoceras* Zittel
1908 *Desmoceras* (*Latidorsella*) Jacob
1925 *Phyllodesmoceras* Spath
1938 *Desmoceras* (*Pseudouhligella*) Matsumoto (*nom. nud.*)
1942*a* *Desmoceras* (*Pseudouhligella*) Matsumoto
1947 *Lunatodorsella* Breistroffer
1954*a* *Onitshoceras* Reyment
1971 *Desmoceras* (*Moremanoceras*) Cobban

Discussion

Wiedmann & Dieni (1968) followed Wright (in Arkell *et al.* 1957) in including *Latidorsella* and *Phyllodesmoceras* within the synonymy of *Desmoceras* s.s., while retaining *Lunatodorsella* and *Pseudouhligella* as valid subgenera.

Desmoceras (*Moremanoceras*) Cobban (type species *Tragodesmoceras scotti* Moreman, 1942: 208, pl. 33 (fig. 8)) was said to differ (Cobban 1971: 5) from *Desmoceras* 'chiefly by having a simpler suture with broad lateral lobe and shorter auxiliary lobes. Constrictions, which are present by the juvenile stages, disappear and then are rejuvenated in the late adult stage.' *Moremanoceras* was also said to resemble the Coniacian *Onitshoceras* in form and sculpture, but with a very different suture-line.

Fig. 15. A. *Calycoceras* (*Calycoceras*) *naviculare* (Mantell), SAM-PCA2764, see also Fig. 11A. B–C. *Puzosia* (*Anapuzosia*) *dibleyi* (Spath). B. SAM-PCA2748. C. SAM-PCA2725. D. *Venitella forbesiana* (Stoliczka), SAM-PCA2795. × 1.

Onitshoceras Reyment (type species *O. matsumotoi* Reyment, 1954*b*: 249, pl. 3 (figs 1–2), pl. 5 (fig. 7)) was diagnosed by Reyment (1955: 19) as follows: 'Flanks slightly inflated, venter broad, gently rounded, umbilicus narrow. Ornament consists of numerous irregular prorsiradiate ribs, swinging forwards and thickening on the venter. In the young they begin at mid-flank, but in the adult at the umbilical margin.'

The differences between *Onitshoceras* and *Desmoceras* are no greater than between the latter and *Moremanoceras*, and consequently Reyment's genus is probably also best treated as a subgenus of *Desmoceras*. The differences between the various subgenera of *Desmoceras* are generally subtle and of questionable taxonomic value. At present they are no more than chronostratigraphic taxa. However, until objective population studies are undertaken, and the intraspecific and ontogenetic variation within the various subgenera better understood, the following subgenera are recognized within *Desmoceras*:

D. (*Desmoceras*). Shell inflated, moderately to very involute, with depressed subquadrate to suboval whorl section. Ornament comprises strong sigmoidal ribs (constrictions on the internal mould), between which are dense growth striae or weak ribs on the outer part of the flanks and venter. Age: Upper Aptian–Upper Cenomanian.

D. (*Lunatodorsella*). Similar to *D.* (*Desmoceras*), but shell cadicone. Doubtfully separable from *Desmoceras* s.s. Age: Upper Albian.

D. (*Pseudouhligella*). Similar to *D.* (*Desmoceras*), but with biconcave constrictions, while whorl section generally compressed in maturity, and frequently with narrowly arched venter. Possibly dimorphic. Suture considerably incised, with symmetrical trifid lateral lobe and numerous auxiliary elements decreasing in size away from the lateral lobe. Age: Upper Albian–Upper Cenomanian.

D. (*Onitshoceras*). Similar to *D.* (*Desmoceras*), but with fine irregular ribs arising near the umbilicus and strengthening across the venter. Suture-line with very narrow lobes and one or more saddles projecting beyond line of suture. Age: Coniacian.

D. (*Moremanoceras*). Similar to *D.* (*Onitshoceras*), but possessing simpler suture, with broad lateral lobe and short auxiliary lobes. Age: Uppermost Cenomanian.

Subgenus *Pseudouhligella* Matsumoto, 1942

Type species *Desmoceras whiteavesi* var. *japonica* Yabe, 1902

Desmoceras (*Pseudouhligella*) aff. *ezoanum* Matsumoto, 1942

Fig. 16

Compare

Desmoceras toucasi Douvillé (*non* Jacob), 1931: 40, pl. 2 (fig. 6a–b).

Desmoceras (*Pseudouhligella*) *ezoanum* Matsumoto, 1942*a*: 26, text-fig. 1b; 1954*b*: 260, pl. 3 (figs 1–4).

Description

Douvillé's (1931) example, the whereabouts of which is unknown, would seem to belong here. Judging from Douvillé's figure (Fig. 16), the specimen clearly has the recrystallized test preserved and is rather involute (umbilicus 25% of the diameter), with a rounded? umbilical shoulder, convex flanks, and a narrowly arched venter. The whorl section is compressed, with maximum width below mid-flank. The shell is ornamented only with flexuous growth striae and frequent, slightly prorsiradiate, flexuous constrictions which are weakly projected across the venter.

Discussion

Unfortunately, the exact characters of the shell cannot properly be judged from Douvillé's figure (Fig. 16), but the Angolan specimen appears to be related to *D.* (*P.*) *ezoanum* Matsumoto (1942*a*: 26, text-fig. 1b; 1954*b*: 260, pl. 3 (figs 1–4)), from which it differs largely in possessing a (?) rounded and not angular umbilical shoulder. In this respect it approaches *D.* (*P.*) *poronaicum* Yabe (Matsumoto 1954*b*: 259, pl. 3 (figs 5–7)) which differs, however, in having an elliptical whorl section. Noteworthy is the fact that Yabe (1902) considered *D.* (*P.*) *poronaicum* possibly a juvenile *D.* (*P.*) *japonicum* Yabe, whilst Matsumoto (1954*b*) at first regarded it as an extreme variant of *D.* (*P.*) *ezoanum*. In Japan, *D.* (*P.*) *japonicum* Yabe, *D.* (*P.*) *poronaicum* Yabe, and *D.* (*P.*) *ezoanum* Matsumoto are contemporaneous species in the Paleogyliakian (Cenomanian); *D.* (*P.*) *poronaicum* is based upon juvenile material (less than 25 mm diameter) which may represent the inner whorls of either *D.* (*P.*) *japonicum* or *D.* (*P.*) *ezoanum*; *D.* (*P.*) *japonicum* is based upon large (118 mm diameter) adult material characterized by frequent constrictions and flat parallel flanks, while *D.* (*P.*) *ezoanum*

Fig. 16. *Desmoceras* (*Pseudouhligella*) aff. *ezoanum* Matsumoto. The specimen figured by Douvillé (1931) as *Desmoceras toucasi* Jacob (after Douvillé 1931). ×1.

is based upon medium-sized (52 mm diameter) adult material which differs from *D.* (*P.*) *japonicum* in that the adult whorls are more compressed, with convergent flanks and a narrowly arched venter, and fewer less prominent constrictions. Matsumoto's (1954*b*) variant, *D.* (*P.*) *japonicum compressior* (= *D.* (*P.*) *japonicum* s.s.) was said to differ from *D.* (*P.*) *ezoanum* only in having flat parallel and not convergent flanks. Clearly these differences are due to a comparison of the juvenile whorls of *D.* (*P.*) *japonicum* with the adult whorls of *D.* (*P.*) *ezoanum*. It is doubtful, therefore, whether the inner whorls of *D.* (*P.*) *japonicum* and *D.* (*P.*) *ezoanum* can be satisfactorily distinguished. The fact that *D.* (*P.*) *ezoanum* attains maturity at smaller diameters than *D.* (*P.*) *japonicum*, and is characterized by a change in shape of the adult whorls would seem to suggest that the differences are those between sexual dimorphs. Clearly, however, objective population studies on the Japanese material are required to confirm this suggestion.

The Upper Albian *D.* (*P.*) *dawsoni* Whiteaves (1884: 205, pl. 26 (fig. 1); 1900: 286, pl. 37 (fig. 3)) is more strongly compressed, with a narrower umbilicus (14–16% of diameter) and higher whorls, but the differences are slight. Material figured by Matsumoto (1959*a*) from Alaska clearly shows constrictions to increase in number and prominence on the body chamber.

Desmoceras (*Pseudouhligella*) *calabarense* Reyment (1955: 18, pl. 2 (fig. 8), pl. 3 (fig. 1)) was said to differ from *D.* (*P.*) *japonicum* only in being more evolute and in having less strongly flexed constrictions. The latter clearly become more flexuous on the body chamber (cf. Matsumoto 1959*a*) and hence the Nigerian species differs only in having a slightly wider umbilicus (19% at 53 mm diameter as opposed to 14–15% in *D.* (*P.*) *japonicum*). For the present, the Nigerian species is best treated as a subspecies of *D.* (*P.*) *japonicum* although population studies may show even such a separation to be superfluous.

Superfamily ACANTHOCERATACEAE Hyatt, 1900
Family **Acanthoceratidae** Hyatt, 1900
Subfamily Mantelliceratinae Hyatt, 1903
Genus *Calycoceras* Hyatt, 1900
Type species *Ammonites navicularis* Mantell, 1822

1900 *Calycoceras* Hyatt
1926 *Metacalycoceras* Spath
1959 *Lotzeites* Wiedmann
1972 *Conlinoceras* Cobban and Scott
1972 *Gentoniceras* Thomel
1972 *Newboldiceras* Thomel
1972 *Subeucalycoceras* Thomel
1972 *Mourreiceras* Thomel

Discussion

Within recent years the rather broadly perceived genus *Calycoceras* has been subdivided into a number of subgenera (and genera).

The genus *Metacalycoceras* Spath (1926) was proposed for the specimen of *Ammonites navicularis* figured by d'Orbigny (1842, pl. 103). However, according to the Code of Zoological Nomenclature (p. 59), the type of 'a nominal genus is a *nominal* species' and hence *Metacalycoceras* becomes a junior objective synonym of *Calycoceras*.

Lotzeites Wiedmann (type species *Acanthoceras aberrans* Kossmat, 1895: 202, pl. 14 (fig. 4)) was erected for small *Cheloniceras*-like homeomorphs, with a coronate whorl section and moderately wide umbilicus. Distant flank ribs are ornamented with sharp, pointed umbilical bullae and prominent lower ventro-lateral tubercles. The latter are joined across the broad, convex venter by paired ribs, between which is an intercalary. All ribs are ornamented with weak upper ventro-lateral and siphonal tubercles. As pointed out by Kennedy (1971: 70), however, some species referred to *Lotzeites*, e.g. *C.* (*L.*) *bathyomphalum* (Kossmat), have outer whorls indistinguishable from *C. subgentoni* (Spath) while 'there is every transition from *bathyomphalum* type nuclei to *subgentoni* type nuclei in contemporary populations from the Middle Cenomanian of southern England'. Moreover, according to Kennedy & Juignet (1973), the holotype of *Calycoceras* (*Lotzeites*) *crassum* Thomel appears to be a poorly preserved *Acanthoceras hippocastanum* (J. de C. Sowerby).

Gentoniceras Thomel (type species *Ammonites gentoni* Brongniart, 1822: 150, pl. 11 (fig. 6a–b)) was proposed as a subgenus of *Calycoceras* for forms characterized by having a much more compressed whorl section than *Calycoceras* s.s., with dense ribbing which is always dominant over the tuberculation. Ventral tuberculation is weak, with lower ventro-lateral and siphonal tubercles frequently lost at an early stage. *C.* (*Gentoniceras*) may be a synonym of the earlier *C.* (*Hourcquiceras*) Collignon (1939) (see discussion under Euomphaloceratinae).

Calycoceras s.s. was diagnosed by Thomel (1972) as comprising strongly inflated forms, always with a very depressed whorl section and with prominent, robust ribbing. Ventral tuberculation weakens considerably on the outer whorls or may even be lost completely.

Newboldiceras Thomel (type species *Acanthoceras newboldi* Kossmat, 1897: 111, pl. 12 (figs 2–3), pl. 14 (fig. 2)) was erected as a new genus within the Acanthoceratinae for *Calycoceras*-like homeomorphs in which the whorl section is compressed, subquadratic. As in *Calycoceras* s.l., ribbing is generally fine and masked by the tubercles at early growth stages. Unlike *Calycoceras*, siphonal tubercles are retained to large diameters. Its characters are 'quelque sorte hybrides entre ceux des genres *Calycoceras* et *Acanthoceras*'. It is as yet uncertain whether this group comprises mantelliceratinid homoeomorphs of *Acanthoceras* or acanthoceratinid homoeomorphs of *Calycoceras*. At present, the writer is inclined to treat *Newboldiceras* as a subgenus of *Calycoceras*.

Within *Newboldiceras*, Thomel (1972) erected the subgenera *Subeucalycoceras* (type species *Acanthoceras baylei* Pervinquière, 1907=*Acanthoceras sarthacense* Bayle, 1878: pl. 62 (figs 1–2)) and *Mourreiceras* (type species *N.* (*M.*) *mourrei* Thomel, 1972: 118, pl. 48). *Subeucalycoceras* was proposed for forms

with flat, subparallel flanks and dense, rather straight, rursiradiate ribbing, the flanks forming a right angle with the venter. Judging from Bayle's (1878) figure, however, *N.* (*S.*) *baylei* (Pervinquière) appears to be a *Gentoniceras*. *Mourreiceras* was erected for denser and more finely ribbed forms homoeomorphous with *Euomphaloceras*, but probably does not bear separation from *Newboldiceras* sensu stricto.

Conlinoceras (type species *Calycoceras* (*Conlinoceras*) *gilberti* Cobban & Scott, 1972: 61, pl. 1, pl. 2 (figs 5–9, 13–18), pl. 3 (figs 5–7, 11)) was proposed as a subgenus of *Calycoceras* for distantly ribbed forms, with a sloping umbilical wall and poorly developed umbilical tubercles.

Within the genus *Calycoceras* sensu lato it now appears possible to recognize the following subdivisions:

C. (*Calycoceras*). Strongly inflated forms with a very depressed whorl section and coarse, robust, rursiradiate ribbing, generally with prominent umbilical bullae. In some species, weakly developed ventral tuberculation persists to maturity. Age: Upper Middle Cenomanian–Uppermost Cenomanian.

C. (*Lotzeites*). Small, *Cheloniceras* homoeomorphs with ribbing looped across the venter between prominent lower ventro-lateral tubercles. Between looped ribs are intercalatories. There are three rows of weakly developed tubercles along the venter. Age: Upper Cenomanian.

C. (*Conlinoceras*). Rather compressed forms with coarse distant ribbing, a sloping umbilical wall and poorly developed umbilical bullae. Ventral tuberculation becomes obsolete at large growth stages. Age: Middle Cenomanian.

C. (*Newboldiceras*). Compressed forms with flattish flanks and a subquadrate whorl section. Ribbing rather fine, dense, masked by tuberculation on inner whorls. Ventral tubercles persist to large diameters and thus homoeomorphous with *Acanthoceras*. Age: Middle–low Upper Cenomanian.

C. (*Gentoniceras*). Compressed forms commonly with strongly tuberculate inner whorls and strongly ribbed, non-tuberculate outer whorls. Umbilicus wide, with steep umbilical walls and prominent umbilical bullae. Age: Middle Cenomanian.

Calycoceras (*Calycoceras*) *naviculare* (Mantell, 1822)

Figs 4L–M, 12A, 15A, 17, 18A–B

Ammonites navicularis Mantell, 1822: 198, pl. 22 (fig. 5). Stoliczka, 1864: 73, pl. 39 (figs 2–4). Crick 1919: 154, pl. 4.
Acanthoceras naviculare (Mantell) Kossmat, 1897: 11. Choffat, 1898: 72, pl. 4 (fig. 6a–b), pl. 6 (figs 1–2).
Fagesia navicularis (Mantell) de Grossouvre, 1912: 26, pl. 3 (fig. 1).
Metacalycoceras grossouvrei Spath, 1926: 431.
?Metacalycoceras boehmi Spath, 1926: 431.
Acanthoceras borgesi Douvillé, 1931: 32, pl. 2 (figs 3–4).
Calycoceras (*Metacalycoceras*) *stoliczkai* Collignon, 1937: 48.

Calycoceras naviculare (Mantell) Hyatt, 1900: 589; 1903: 113. Spath, 1923: 144; 1937: 278. Wright & Wright, 1951: 26. Arkell *et al.*, 1957: L431, fig. 531, 6, fig. 532. Cobban, 1971: 13, pl. 1 (figs 1–3), pl. 10 (figs 1–8), pl. 11 (figs 1–5), pl. 12 (figs 1–2), pl. 13 (figs 1–5), pl. 14 (figs 1–3), pl. 15 (figs 1–2), pl. 16 (figs 1–2), pl. 17. Kennedy 1971: 71, pl. 33 (fig. 1a–b), pl. 34 (fig. 1a–b), pl. 35 (figs 1–2), pl. 36 (figs 1–4), pl. 37 (figs 1–3), pl. 47 (figs 1a–c, 3a–b, 5a–b). Thomel 1972: 53.
Calycoceras borgesi (Douvillé) Wright & Wright, 1951: 26. Thomel, 1972: 55.
?Calycoceras obrieni Young, 1957: 1171, pl. 150 (figs 1–4).
Calycoceras (*Metacalycoceras*) *auspicum* Anderson, 1958: 243, pl. 20 (fig. 8).
Mantelliceras oregonense Anderson, 1958: 244, pl. 8 (fig. 4), pl. 14 (fig. 1).
Calycoceras stoliczkai Collignon, Matsumoto, 1959*b*: 78, pl. 21 (fig. 1). Thomel, 1972: 56, pl. 17 (figs 8–10), pl. 18 (figs 5–7).
?Calycoceras boehmi (Spath) Wright & Wright, 1951: 26.
Calycoceras grossouvrei (Spath) Collignon 1965: 10, pl. 3 (fig. 2).

Diagnosis

A coarsely ribbed, evolute (umbilicus 23–32% of diameter) *Calycoceras*, generally strongly inflated and commonly with a very depressed whorl section. There are between 30 and 50 rursiradiate ribs per whorl (rectiradiate in juveniles), generally alternating long and short. Except for prominent umbilical bullae on the long ribs and ventro-lateral angulations on some specimens, tuberculation is absent except at small growth stages (generally less than 50 mm diameter).

Description

This is a common form in the Angolan fauna, and all specimens have the recrystallized test preserved.

The shell is strongly inflated (W/H = 1,31–1,68), with a deep, rather narrow umbilicus (22–30% of diameter), and broad, convex, slightly overhanging umbilical walls. The whorl section (Fig. 17) is strongly depressed, reniform, with a broadly rounded venter sometimes showing ventro-lateral angulations. Rectiradiate to slightly rursiradiate ribs begin at the umbilical seam and terminate in prominent bullae on the umbilical shoulder. From the bullae arise coarse, robust, slightly rursiradiate flank ribs which alternate with shorter intercalatories arising

Fig. 17. *Calycoceras* (*Calycoceras*) *naviculare* (Mantell). Whorl sections. A. SAM–PCA2715. B. SAM–PCA2764. ×1.

somewhat below mid-flank. There are generally about 30 ribs per whorl on the outer whorls, although juvenile whorls are somewhat more densicostate with up to 36 ribs per whorl. Ribs are broader than the interspaces. Ribs arising from a bulla on one flank are commonly intercalated on the opposing flank. In all the Angolan material, ranging from 34 mm to 115 mm in diameter, ventral tuberculation appears to be lacking, although distinct ventro-lateral angulation of the ribbing is present to large diameters.

Measurements

No.	D	H	Wc	Wi	Wi/H	Ui	Uo
SAM–PCA2717	87	32 (37)	46 (53)	42 (42)	3,31	?	42
SAM–PCA2715	84	35 (42)	58 (69)	53 (63)	1,51	25 (30)	44
,,	53	25 (47)	43 (81)	42 (79)	1,68	15 (28,6)	?
,,	34	?	26	?	?	9 (26,4)	16
SAM–PCA2723	95	40 (42)	58 (61)	54 (57)	1,35	26 (27,3)	45
,,	73	31 (42)	45 (62)	41 (56)	1,32	21 (28,7)	35
SAM–PCA2733	72	35	?	?	?	16 (22,2)	39
SAM–PCA2762	34	16 (47)	22 (64)	21 (62)	1,31	10 (30)	17
SAM–PCA2764	115	48 (42)	73 (63)	63 (55)	1,31	30 (26)	46

Discussion

The degree of inflation and the rib density of the Angolan material seem to be rather variable. The confusion which has long surrounded Mantell's species has recently been clarified by Cobban (1971: 13) and Kennedy (1971: 72). The writer cannot agree with Thomel's (1972) finely drawn species limits and thus follows the previous authors in their treatment of this species.

Calycoceras boulei Collignon (1937: 43, pl. 5 (figs 2–4), pl. 8 (figs 9–11)) is a somewhat earlier form, first appearing late in the Middle Cenomanian, and differing largely in the retention of upper and lower ventro-lateral tubercles to large diameters.

Calycoceras guerangeri (Spath) was originally figured only in side view (Gueranger 1867, pl. 4 (fig. 4)) and without seeing the holotype, which is still extant, it is difficult to assess. As interpreted by Thomel (1972: 61) this species differs in being of somewhat earlier age, with a more compressed whorl section and 2–3 intercalatories between main ribs.

Calycoceras bruni (Fabre) (1940: 230, pl. 8 (figs 1–2)), the type of which is apparently lost (Thomel 1972: 60), shows the following features: shell inflated, with a depressed whorl section, and about 30 strong, slightly rursiradiate ribs on the outer whorl. On the adapical portion of the outer whorl, the ribs are slightly flexuous whereas adorally they are rigid. Main ribs arise from prominent umbilical bullae and are separated by 1–2 intercalatories. All ribs are ornamented with ventro-lateral and siphonal tubercles to large growth stages; but lateral tubercles appear to be lacking. It differs from *C. naviculare*, therefore, in being of older age and in the persistence of ventral tuberculation to large diameters.

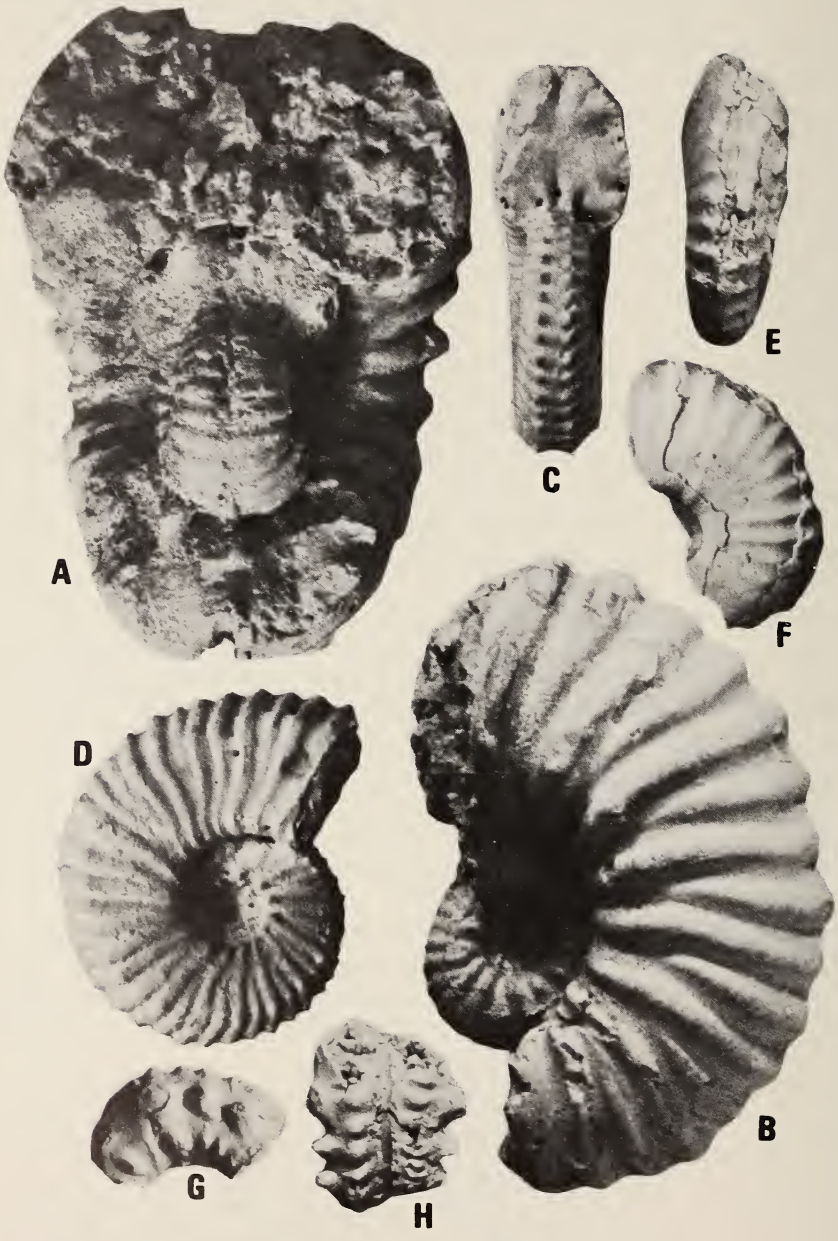

Fig. 18. A–B. *Calycoceras* (*Calycoceras*) *naviculare* (Mantell), SAM–PCA2715. C–D. *Watinoceras coloradoense* (Henderson) (♀), SAM–PCA2730. E–F. *Pseudocalycoceras angolaense* (Spath), SAM–PCA2808. G–H. *Euomphaloceras* (*Kanabiceras*) *septemseriatum* (Cragin), SAM–PCA2826. Note the (?)superficial resemblance to *Metasigaloceras*. ×1

Calycoceras robustum Thomel (1972: 63, pl. 19 (figs 1–5)) is a compressed form with robust, rursiradiate ribbing. Main ribs arise from prominent umbilical bullae and alternate with shorter intercalatories. Occasionally there are 2 intercalatories between main ribs, with about 30 ribs on the outer whorl. Main ribs have lateral tubercles, while all ribs are ornamented with ventro-lateral and siphonal tubercles.

Calycoceras letullieri Collignon (1964: 131, figs 1603–1604) is a strongly inflated form belonging to the *boulei* group. On the outer whorl there are 32 ribs, generally alternating long and short. Long ribs are ornamented with prominent umbilical, lateral, ventro-lateral and weak siphonal tubercles at small growth stages, but only the umbilical and lateral tubercles are retained to maturity.

While the differences between *C. boulei*, *C. bruni*, *C. letullieri* and *C. robustum* are probably no more than the intraspecific variation observed in *C. naviculare*, the author hesitates to place the first 4 species into synonymy until objective population studies have been made. They form a closely related group of slightly older species, generally less inflated, in which ventral tuberculation is retained to large diameters.

Calycoceras thieuloyi Collignon (1964: 133, figs 1605–1607) is a strongly inflated globose species. In the holotype, 22 prominent umbilical bullae give rise to coarse, robust, rursiradiate primary ribs with sporadic intercalatories, so that there were probably about 36 ribs on the outer whorl. At early growth stages there may be up to 3 intercalatories between main ribs. Lateral and ventral tuberculation is lacking at all growth stages figured. According to Kennedy (1971: 73), this species may be a *Mantelliceras*.

In time, there may be some justification for recognizing a number of subspecies within *C. naviculare*. At present, however, population studies are not far enough advanced to allow such a grouping.

Occurrence

At present, *C. naviculare* is recorded from Japan, the Western Interior, California, Texas, England, France, Portugal, Angola, Madagascar and southern India.

Subfamily Acanthoceratinae Hyatt, 1900
Genus *Protacanthoceras* Spath, 1923
Type species *Ammonites bunburianus* Sharpe, 1853

Protacanthoceras? sp. A

Fig. 19C–D

Compare

Ammonites bunburianus Sharpe, 1853: 25, pl. 9 (fig. 3a-c). Pictet & Campiche, 1860: 315. Diener, 1925: 24.

Protacanthoceras bunburianum (Sharpe) Spath, 1923: 144. Kennedy, 1971: 97 pl. 31 (fig. 1a-c).

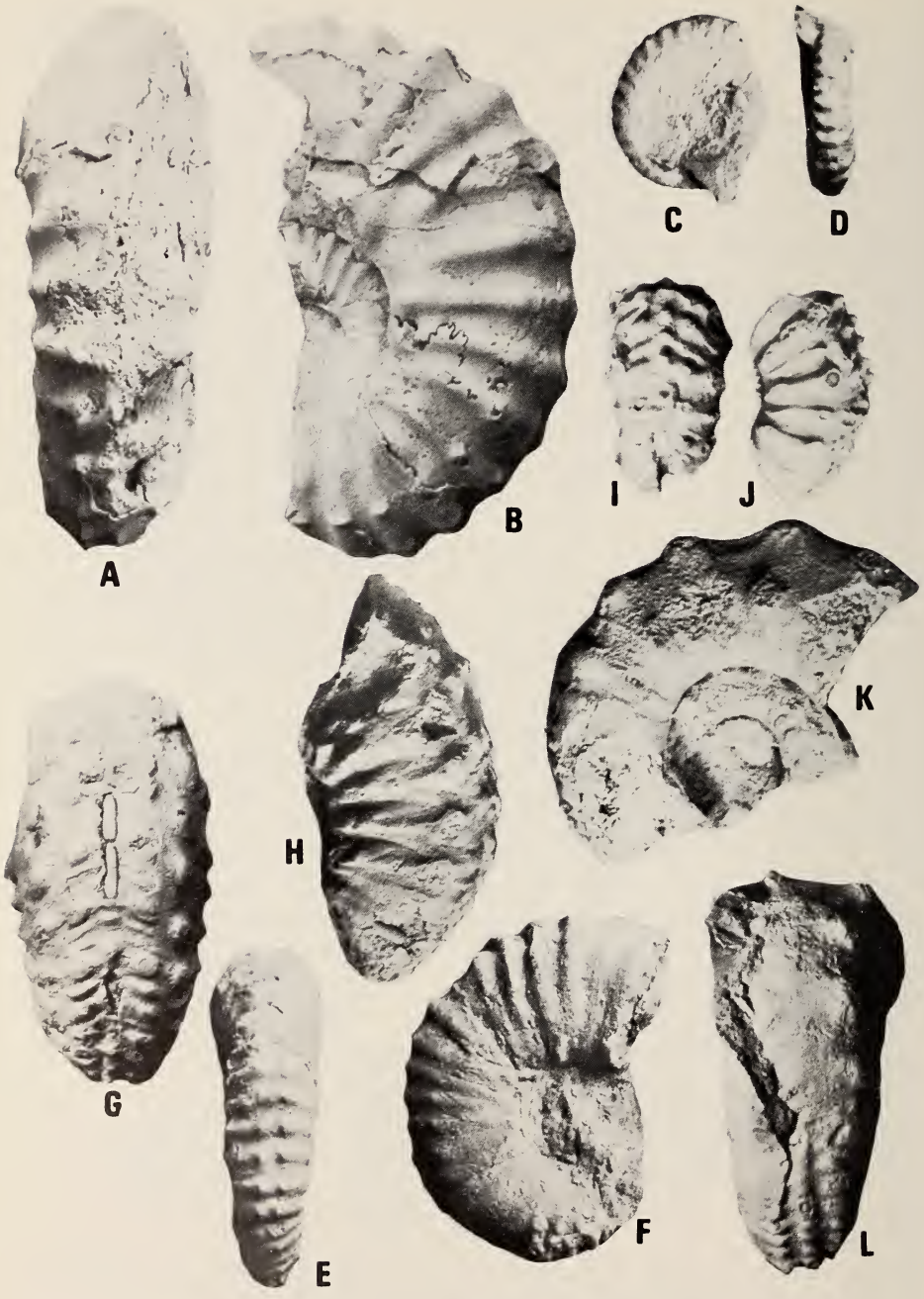

Fig. 19. A–B. *Pseudocalycoceras angolaense* (Spath). An internal mould, SAM–PCA2734. C–D. ?*Protacanthoceras* sp., SAM–PCA2778. E–F. *Watinoceras coloradoense* (Henderson) (♀), SAM–PCA2753. G–L. *Euomphaloceras* (*Kanabiceras*) *septemseriatum* (Cragin). G–H. SAM–PCA2736. Note prominent umbilical bullae, break-up of keel into isolated tubercles, and virtual disappearance of ventral sulci. I–J. SAM–PCA2756. K–L. SAM–PCA2742, a (?)pathological specimen showing abrupt loss of ventral ornament. XI.

Description

A single, rather poorly preserved example, with the recrystallized test preserved, shows affinities to Sharpe's species.

The shell is strongly compressed (W/H = 0,66), involute, with flat, parallel flanks and a narrow umbilicus (22% of diameter). The venter is narrow, with an evenly rounded intercostal section, and is ornamented by three rows of closely spaced, weakly clavate tubercles situated on weak ribs. The lower ventro-lateral tubercles are very indistinct. Ribbing seems to be lacking on the lower flanks, first appearing at the lower ventro-lateral tubercle and becoming distinct only across the venter. On the outer whorl, there are about 18 ribs across the venter per half whorl.

Measurements

No.	D	H	W	W/H	Ui
SAM–PCA2778	23	9 (39)	6 (26)	0,66	5 (22)

Discussion

The above specimen is only tentatively referred to this genus because of its poor preservation. From what can be seen of the Angolan example, it cannot be distinguished from *P. bunburianum*. The author's reservations stem from the fact that laterally crushed inner whorls of *Pseudocalycoceras angolaense* would probably be equally difficult to distinguish from *P. bunburianum*.

Protacanthoceras? sp. B

Fig. 14D–E

Description

This specimen is also tentatively assigned to *Protacanthoceras*, although the preservation leaves much to be desired.

It is small, involute and compressed, but appears to be laterally crushed. The little that is preserved of the ornament shows there to have been rather prominent rectiradiate ribs, at least on the outer flanks, with small umbilical and lower ventro-lateral tubercles and three rows of clavi closely spaced across the venter.

Discussion

The relatively coarse ribbing of this example would appear to distinguish it from juveniles of *Pseudocalycoceras angolaense* (Spath). Consequently, the rather coarse ornament is taken to indicate closer affinities with *Protacanthoceras* than *Pseudocalycoceras*.

Protacanthoceras compressum (Jukes-Browne) is similar, but has fewer more prominent ribs, with distinct umbilical and lower ventro-lateral tubercles.

Genus *Tarrantoceras* Stephenson, 1955

Type species *Tarrantoceras rotatile* Stephenson, 1955

1955 *Tarrantoceras* Stephenson
1969 *Sumitomoceras* Matsumoto

Discussion

Tarrantoceras was originally (Stephenson 1955: 59) separated from *Eucalycoceras* on differences in the suture-line. In the emended diagnosis given by Cobban & Scott (1972: 64), this genus comprises moderately large, compressed forms (Fig. 20) in which prominent prorsiradiate flank ribs are ornamented with umbilical, upper and lower ventro-lateral and siphonal tubercles. Of these, the upper ventro-lateral tubercles are the most prominent, rising above the level of the siphonal tubercles. The latter are very weakly developed in the adult growth stages and are finally lost about half-way up the body chamber, while the lower ventro-lateral tubercles are lost at the start of the body chamber.

Fig. 20. *Tarrantoceras rotatile* Stephenson. The holotype, after Stephenson (1955). ×1.

Sumitomoceras Matsumoto (in Matsumoto *et al.* 1969: 283) was erected for moderately evolute forms with flat flanks and a compressed whorl section. Long ribs arise from umbilical tubercles and are separated by 1–2 intercalatories. All ribs are prorsiradiate and ornamented with upper and lower ventro-lateral tubercles, while at very immature growth stages weak siphonal tubercles are present. In the middle and late growth stages the ventro-lateral tubercles weaken and disappear, constrictions develop and this genus homoeomorphs *Kossmaticeras*.

However, the holotype of *Tarrantoceras multicostatum* Stephenson (1955: 61, pl. 6 (figs 21–23)), considered a synonym of *T. rotatile* Stephenson by Cobban

& Scott (1972), shows the same loss of tuberculation on the body chamber as does *Sumitomoceras*, whilst the juvenile whorls are also comparable. The author regards *Sumitomoceras* as a junior subjective synonym of *Tarrantoceras*.

Another genus closely allied to *Tarrantoceras* is *Eucalycoceras* Spath. As diagnosed by Kennedy (1971: 80), this genus comprises involute forms with compressed whorls and broad flattish flanks. Ribbing is rather dense, generally with umbilical, upper and lower ventro-lateral and siphonal tubercles. At large growth stages, some or all of the ventral tubercles may be lost. *Tarrantoceras* is thus very close to *Eucalycoceras*. Besides the sutural differences noted by Stephenson (1955), *Tarrantoceras* seems invariably to lose its siphonal tubercle and to be adult at smaller diameters than *Eucalycoceras*, whilst the latter genus is typically higher-whorled and more involute.

Other Upper Cenomanian genera with five rows of tubercles across the venter are the micromorph *Protacanthoceras* and *Pseudocalycoceras*, the latter distinguished by its flexuous, rursiradiate ribbing.

Tarrantoceras? sp. juv. indet.

Fig. 21D–E

Description

A single small, fragmentary specimen with recrystallized test preserved is assigned to this genus.

The shell is moderately compressed, with a polygonal costal and rounded intercostal section. It would appear to have been moderately evolute. There are small but distinct umbilical tubercles from which arise prorsiradiate main ribs. Between long ribs there is almost invariably a short rib intercalated at about mid-flank. All ribs bear prominent lower ventro-lateral tubercles and slightly clavate upper ventro-lateral and siphonal tubercles.

Discussion

The solitary Angolan fragment closely resembles juvenile forms of *Eucalycoceras*, such as were figured by Kennedy (1971). So far as the author is aware, however, this genus has not been recorded from strata of this age (top Cenomanian), and thus he prefers to refer the Angolan specimen to the closely allied *Tarrantoceras*.

At a similar growth stage, *Pseudocalycoceras angolaense* (Spath) is very weakly ribbed or smooth, while species of *Protacanthoceras* lack the strong flank ribbing seen in the Angolan specimen.

Genus *Pseudocalycoceras* Thomel, 1969

Type species *Ammonites harpax* Stoliczka, 1864

1969 *Pseudocalycoceras* Thomel
1969 *Neocalycoceras* Thomel
1972 *Pseudocalycoceras* (*Haugiceras*) Thomel

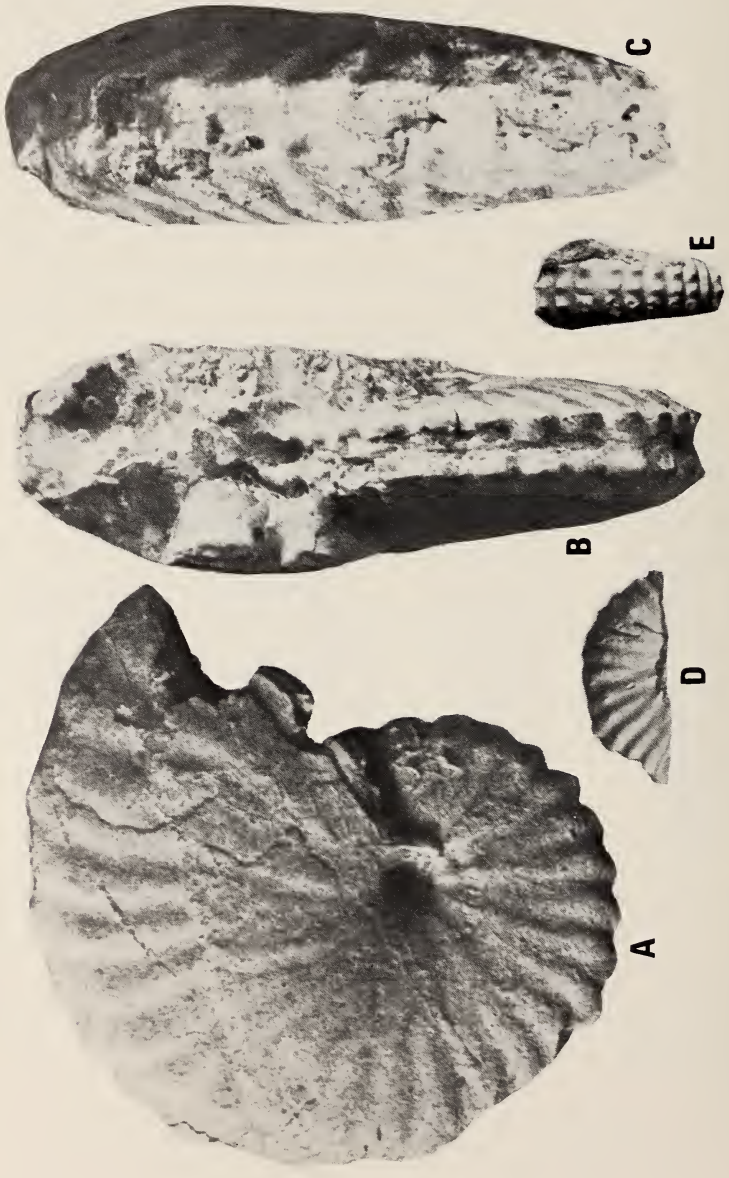

Fig. 21. A–C. *Metoicoceras gibbosum* Hyatt, SAM-PCA2714. Note very weak umbilical bullae.
D–E. *Tarrantoceras* sp. juv., SAM-PCA2784. × 1.

Discussion

This genus was erected (Thomel 1969: 651) for moderately evolute forms with coarse rursiradiate, flexuous ribbing and five rows of tubercles across the venter. Differences from other genera are noted under the discussion of *Watinoceras*.

Neocalycoceras was erected without description or diagnosis and is thus a *nomen nudum*. *Haugiceras* (type species *Acanthoceras haugi* Pervinquière, 1907: 270, pl. 14 (fig. 1a–b)) (Fig. 22) was proposed as a subgenus of *Pseudocalycoceras* for rather inflated forms in which the whorl section was wider than high, the ribs were more rigid and less robust, rursiradiate, but less recurved than in *Pseudocalycoceras* s.s. The tuberculation was said to be entirely different, in *Haugiceras* the umbilical tubercles are not twisted into an S, while the tubercles across the venter are rounded and not clavate, and closer together. Into this subgenus, Thomel (1972) placed *Pseudocalycoceras angolaense* (Spath), *P. haugi* (Pervinquière) and *P. robustum* Thomel. However, Thomel's separation of *Haugiceras* from *Pseudocalycoceras* appears to be artificial, and the author regards the two names as synonyms.

Fig. 22. *Pseudocalycoceras haugi* (Pervinquière). The holotype, after Pervinquière (1907). ×1.

Thomel (1972) also included a number of typical *Pseudocalycoceras* species under his heterogenous group of *Eucalycoceras* (*Proeucalycoceras*) (type species *Calycoceras* (*Eucalycoceras*) *besairiei* Collignon, 1937: 13, pl. 3 (figs 1–4), pl. 8 (fig. 5)). This subgenus was erected for moderately evolute forms with a compressed, quadrate whorl section, flat flanks, and dense, fine, flexuous ribbing at immature growth stages. Ribs are ornamented with small umbilical bullae, upper and lower ventro-lateral tubercles, of which the former are more prominent, and siphonal tubercles which are lost at an early stage. Of the species assigned to this subgenus, *Tarrantoceras bentonianum* (Cragin), *Pseudocalycoceras dentonense* (Moreman) and its synonym *P. lewisvillense* (Moreman) (cf. Cobban & Scott 1972), together with *Calycoceras leonense* (Adkins) and *Mantelliceras lymense* (Spath) do not belong here. As presently defined, this taxon (*Proeucalycoceras*) is of little value.

Pseudocalycoceras angolaense (Spath, 1931)

Figs 4A–C, H–K, 6I–J, 10F–G, 14A, 18E–F
19A–B, 23–25, 26F–K

Acanthoceras rhotomagense Taubenhaus (*non* Brongniart), 1920: 13.
Acanthoceras sp. A, Moreman, 1927: 95, pl. 15 (fig. 2).
Acanthoceras lyelli Douvillé (*non* Leymerie), 1931: 31, pl. 1 (fig. 1).
Protacanthoceras angolaense Spath, 1931: 316. Basse, 1940: 448, pl. 6 (fig. 3). Avnimelech & Shoresh, 1962: 531.
Eucalycoceras dentonense Moreman, 1942: 205, pl. 33 (figs 4–5), text-fig. 2k. Matsumoto, 1959*b*: 97, text-fig. 51.
Eucalycoceras indianense Moreman, 1942: 206, pl. 33 (figs 9–10), text-fig. 21. Matsumoto, 1959*b*: 98.
Eucalycoceras lewisvillense Moreman, 1942: 206, pl. 33 (figs 6–7), text-fig. 2n, u.
Eucalycoceras underwoodi Powell, 1963*a*: 315, pl. 31 (fig. 17).
Pseudocalycoceras (*Neocalycoceras*) *angolaense* (Spath) Thomel, 1969: 651.
Eucalycoceras (*Proeucalycoceras*) *dentonense* Moreman, Thomel, 1969: 650.
Eucalycoceras (*Proeucalycoceras*) *lewisvillense* Moreman, Thomel, 1969: 650.
'*Protacanthoceras*' *angolaense* Spath, Kennedy, 1971: 115.
Pseudocalycoceras angolaense (Spath) Cooper, 1972: 248; 1974: 86.
Pseudocalycoceras (*Haugiceras*) *angolaense* (Spath) Thomel, 1972: 97.
Pseudocalycoceras dentonense (Moreman) Cobban & Scott, 1972: 63, pl. 13 (figs 11–29), pl. 15 (figs 1–7, 10–13).
Pseudocalycoceras sp. aff. *P. dentonense* (Moreman) Matsumoto & Kawano, 1975: 13, pl. 1 (fig. 1), text-fig. 3.

Description

The shell is moderately evolute (umbilicus 18–41 % of diameter), somewhat compressed (W/H = 0,67–1,12) to slightly depressed, with a fairly wide, deep umbilicus.

The best preserved specimen, SAM–PCA2731 (Fig. 26I–K), retains recrystallized test, and is entirely septate to 57 mm diameter. About one-third of the preceding whorl is covered to just below the lower ventro-lateral clavi by the outer whorl. The umbilicus is fairly broad and deep, with a steep umbilical wall, slightly undercut at the seam, and an abruptly rounded umbilical shoulder. The

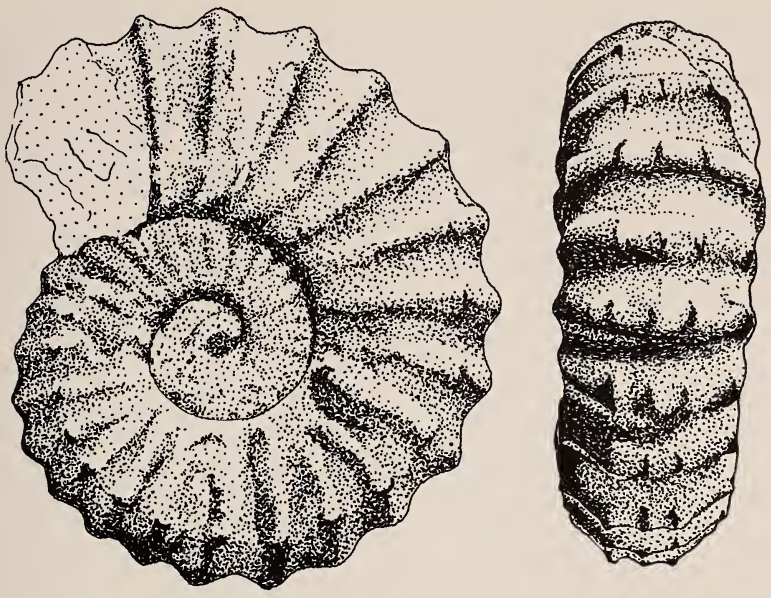

Fig. 23. *Pseudocalycoceras angolaense* (Spath). The holotype (after Douvillé 1931). ×1.

whorl section is slightly compressed, almost quadrate, with a polygonal costal section.

On the outer whorl of SAM–PCA2731, about 18 ribs are weakly developed on the umbilical wall and pass radially to the umbilical shoulder where they give rise to 1–2 flank ribs. The umbilical tubercles are irregularly developed, and there are only 12 on the outer whorl. The flank ribs are flexuous, rursiradiate, and number about 30 on the outer whorl. At the prominent lower ventro-lateral clavi the ribs flex forwards to the upper ventro-lateral clavi and then cross the venter transversely. All ribs bear prominent siphonal clavi. The penultimate whorl of this specimen is very weakly ornamented and shows the earliest whorls to have lacked ribbing, at least on the lower portion of the flanks, and umbilical tubercles to a diameter of about 20 mm.

Together with the above specimen, three other examples, SAM–PCA2767, SAM–PCA2777 and SAM–PCA2772, provide an almost complete ontogenetic sequence for this species. In SAM–PCA2767 (Fig. 4J–K) the flanks are entirely smooth to a diameter of 11 mm, at which stage, in SAM–PCA2777 (Fig. 4A–C), ventral tuberculation appears, as well as very faint ventral ribbing. By 15 mm diameter the ribbing has become more prominent, but is still confined to the outer flanks, while the umbilical shoulder bears occasional weak umbilical tubercles. At this stage the whorl section is oval, with slightly convex flanks converging to the narrowly arched venter. In costal section the venter is almost tabulate and trituberculate. In this same specimen the lower ventro-lateral

Fig. 24. *Pseudocalycoceras angolaense* (Spath). Whorl sections.
A. SAM–PCA2731. B. SAM–PCA2767. C. SAM–PCA2732. ×1.

tubercles, although faint, are evident at 15 mm diameter, whereas in SAM–PCA2767 they are still absent at 28 mm diameter, whilst the latter also shows no signs of umbilical tubercles at the same stage. In SAM–PCA2772 (Fig. 26G), at about the same diameter, the umbilical tubercles are weak but noticeable, with upper and lower ventro-lateral and siphonal tubercles. The ribbing is fairly strong but is not connected to the umbilical tubercles. In SAM–PCA2731 the umbilical tubercles become prominent at about 28 mm diameter. At about this same stage the flanks become flat, or slightly convex, and almost parallel, with the greatest width at mid-flank. In this same specimen there are 11 siphonal clavi within 40 mm along the venter at a diameter of 35 mm, but only 6 at 57 mm diameter. In SAM–PCA2734, with about one-third of a whorl of body chamber preserved, there are only 5 siphonal clavi in an equal distance at 68 mm diameter. This specimen also shows, as does the holotype (Fig. 23), the simple, coarse, straight ribbing on the body chamber.

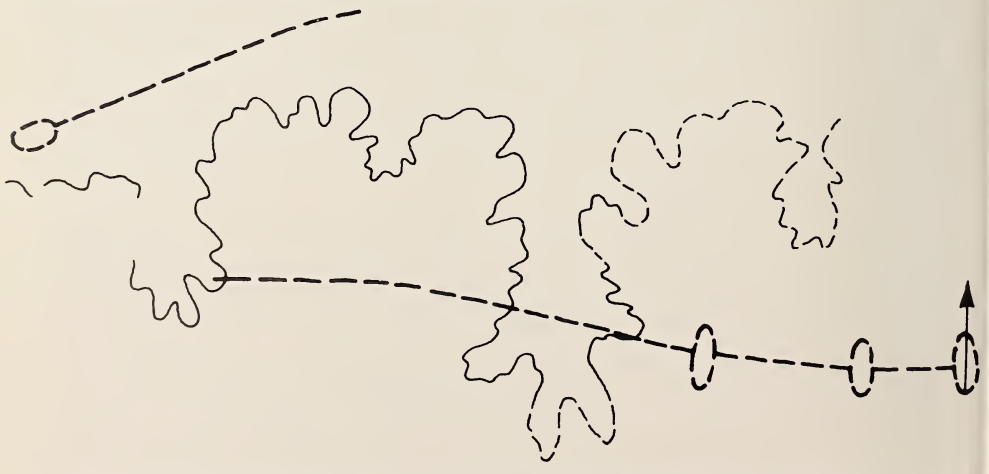

Fig. 25. *Pseudocalycoceras angolaense* (Spath). Suture-line of SAM–PCA2719 at about 60 mm diameter.

A further example, SAM–PCA2721, is coarsely ornamented at an early growth stage, providing further evidence of the great variability in ontogenetic development of this species. It is already showing well-developed umbilical tubercles at a diameter of about 13 mm, while at 25 mm diameter ribbing is already prominent and connected to the umbilical tubercles. This specimen is also slightly more inflated than typical examples.

Measurements

No.	D	H	W	W/H	Uo	Ui
SAM–PCA2731	57	24 (42)	23 (40)	0,96	23	17 (30)
,,	44	21 (48)	20 (45)	0,95	17	13 (30)
SAM–PCA2721	41	16 (39)	18 (44)	1,12	17	12 (29)
,,	29	12 (41)	12 (41)	1,00	12	9 (41)
SAM–PCA2772	37	17 (46)	15 (41)	0,88	15	10 (27)
,,	25	12 (48)	9 (36)	0,75	?	6 (24)
SAM–PCA2777	22	11 (50)	8 (36)	0,73	?	4 (18,2)
,,	15	9 (60)	6 (40)	0,67	?	2 (13,3)
SAM–PCA2734	70	29 (41)	25 (36)	0,86	30	23 (33)
,,	47	22 (47)	?	—	19	14 (30)
SAM–PCA2767	37	13 (35)	10 (27)	0,77	?	9 (24,3)
,,	10	6 (60)	4 (40)	0,67	?	2 (20)

Discussion

Cobban & Scott (1972) have dealt comprehensively with *Pseudocalycoceras dentonense* (Moreman), including *P. lewisvillense* (Moreman) and *P. indianense* (Moreman) within the synonymy of this species. The North American material differs from the Angolan material only in that many individuals have more coarsely ribbed inner whorls, while the ventro-lateral and siphonal tubercles generally weaken and become obsolete between 25 and 80 mm diameter. The differences are clearly not specific, and *P. dentonense* is considered a junior subjective synonym of *P. angolaense*. *Eucalycoceras underwoodi* Powell (1963*a*: 315, pl. 31 (fig. 17)) is a contemporaneous species which also does not bear separation from *P. angolaense*.

Pseudocalycoceras haugi (Pervinquière) (Fig. 22) is more coarsely ribbed, with more prominent umbilical tubercles, less flexuous ribbing, and more swollen lower ventro-lateral tubercles. It represents a larger growth stage than observed in *P. angolaense*, and until its ontogenetic and intraspecific variation is known, I prefer to regard them as distinct.

Thomel (1972) described a number of *Pseudocalycoceras* species from south-east France. Of these, *P. equituriense* Thomel, *P. flandrini* Thomel and *P. planum* Thomel appear better referred to the genus *Thomelites*. *Pseudocalycoceras dromense* Thomel is possibly better assigned to *Lotzeites*. The holotype of *Pseudocalycoceras pseudorbignyi* Thomel was not figured, while the plesiotype is a body chamber fragment which is difficult to assess. According to Thomel

(1972: 95), the holotype is about one-half whorl of an internal mould. The shell is rather evolute (umbilical ratio 32%), with flat subparallel flanks. On the outer whorl, there are 17 flexuous ribs per half whorl, of which 7 arise from bullae at the umbilical shoulder. The venter is narrow and ornamented with three rows of small tubercles.

Pseudocalycoceras robustum Thomel (1972: 98, pl. 47 (figs 6–7)) is a moderately evolute species. The inner whorls (up to 36 mm diameter) are compressed, with the maximum width near the umbilical shoulder. Ornament comprises alternating long and short ribs, rigid, robust, and totalling 25 on the outer whorl. Main ribs arise from prominent, rounded umbilical tubercles, while all ribs are ornamented with upper and lower ventro-lateral and siphonal clavi. At large diameters the siphonal tubercles are lost and the ribs rise to form a sharp crest (? crushed) on the venter. It differs from *P. angolaense* in having more robust, less flexuous ribs which do not arise in pairs from the umbilical shoulder, and is thus probably a junior subjective synonym of *P. haugi*. *Pseudocalycoceras judaicum* (Taubenhaus) (Avnimelech & Shoresh 1962: 531, pl. 15 (fig. 2)) has similar alternating long and short flank ribs, about 16 per half whorl, but is strongly crushed laterally and difficult to compare. It is probably not separable from *P. haugi*.

Pseudocalycoceras harpax (Stoliczka 1865: 72, pl. 39 (figs 1, 1a–b)) is a moderately evolute (umbilical ratio 27–30%), compressed species, with flattish, slightly convex flanks. Main ribs arise from umbilical tubercles (initially rounded but later bullate) and are flexuous, rursiradiate, with 1–2 intercalatories separating main ribs. The evenly rounded venter is ornamented with 5 rows of closely spaced tubercles, upper and lower ventro-lateral and siphonal clavi. There are 38 ribs on the outer whorl, of which 15 are main ribs. This appears to be a Middle or low Upper Cenomanian species which differs from *P. angolaense* in that main ribs do not commonly arise in pairs from the umbilical tubercles, the whorl section is more rounded, not distinctly polygonal as in *P. angolaense*, and the ventral tuberculation is not as prominent nor so markedly clavate. The forms assigned by Thomel (1972) to *P. harpax* and its varieties appear to belong to other species.

Occurrence

Pseudocalycoceras angolaense has been recorded from Texas, the Western Interior, Angola, northern France, Japan and Israel.

Pseudocalycoceras aff. *haugi* (Pervinquière, 1907)

Figs 10H–I, 22, 27

Compare

Acanthoceras haugi Pervinquière, 1907: 270, pl. 14, figs 1a–b.

Protacanthoceras judaicum (Taubenhaus) Avnimelech & Shoresh, 1962: 531, pl. 15 (fig. 1) (holotype refigured).

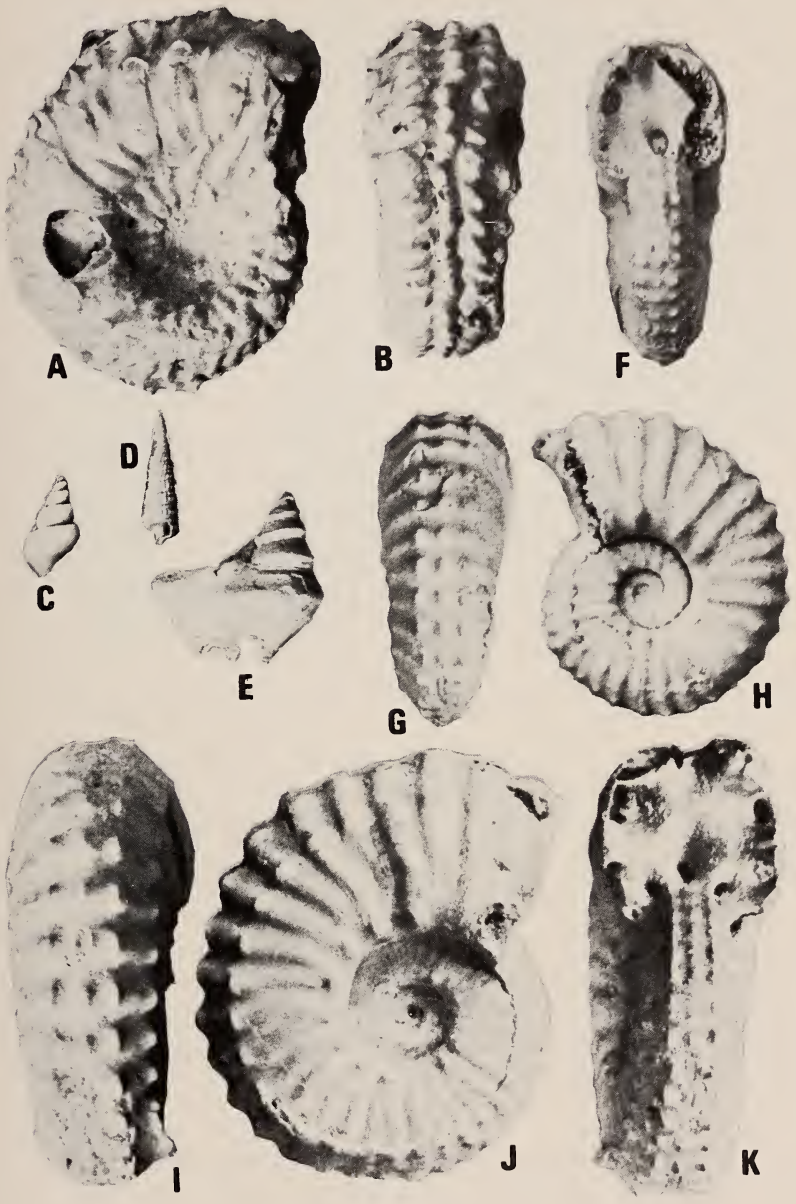

Fig. 26. A–B. *Euomphaloceras* (*Kanabiceras*) *septemseriatum* (Cragin), SAM–PCA2827, ×1. C–E. Undetermined gasteropods. F–K. *Pseudocalycoceras angolaense* (Spath), × 1. F–H. SAM–PCA2721. I–K. SAM–PCA2731.

Protacanthoceras aff. *compressum* Avnimelech & Shoresh (*non* Jukes-Browne), 1962: 532, pl. 15 (fig. 2).
Pseudocalycoceras (*Haugiceras*) *robustum* Thomel, 1972: 98, pl. 47 (figs 6–7).

Description

A rather poorly preserved Angolan example shows affinities to Pervinquière's species. The preservation of the Salinas material, together with the fact that the Tunisian form represents a different ontogenetic stage, makes comparison difficult. The specimen has the recrystallized test preserved.

The Angolan example is strongly compressed and moderately evolute, with about half the preceding whorl covered. The umbilicus is fairly wide and rather shallow, with a steep umbilical wall and subrounded umbilical shoulder. The flanks are broad and flat, almost parallel, with a narrow, evenly rounded venter intercostally, but polygonal costally. The venter is ornamented with three rows of closely spaced clavi. The flank ornament is seen to comprise almost radial, alternating long and short ribs, although there may occasionally be two intercalatories between main ribs. All the ribs have weakly developed lower ventro-lateral tubercles and prominent upper ventro-lateral and siphonal clavi, while the long ribs also have sporadic, faint umbilical tubercles. The last rib on the adoral portion of the outer whorl shows a fairly distinct umbilical tubercle, which would seem to suggest that they became more prominent with age. There are about 15 ribs per half whorl on the outer whorl.

Measurements

No.	D	H	W	W/H	Ui
SAM–PCA2775	32	16 (50)	10 (31)	0,63	8 (25)
,,	25	11 (44)	7 (28)	0,64	6 (24)

Discussion

As noted under the discussion of *P. angolaense*, the species *P. haugi*, *P. robustum* and *P. judaicum* (Fig. 27) are probably not specifically separable, while the above material differs from *P. angolaense* in being more coarsely ornamented at small diameters, with less flexuous, rigid flank ribs. The close resemblance to *P. judaicum* probably relates to the fact that the Angolan material has also been laterally crushed. *Pseudocalycoceras harpax* (Stoliczka) has denser, flexuous ribbing.

Occurrence

Pseudocalycoceras haugi appears to be present in Tunisia, southern France, Israel and possibly Angola.

Subfamily Euomphaloceratinae. **New subfamily**

Diagnosis

Multituberculate derivatives of *Acanthoceras*, typically evolute, with a depressed, subquadrate to compressed, elliptical whorl section, and more or less

Fig. 27. *Pseudocalycoceras* cf. *haugi* (Pervinquière). × 1. The holotype of *Protacanthoceras judaicum* (Taubenhaus), after Avnimelech & Shoresh (1962). × 1.

prominent constrictions on the early whorls. In almost all genera, there are umbilical, upper and lower ventro-lateral and siphonal tubercles, which in some genera are supplemented by one to two rows of lateral tubercles. Range: Middle Cenomanian (possible, but doubtful, Lower Cenomanian mèmbers are discussed below) to uppermost Turonian.

Discussion

As herein interpreted, the Euomphaloceratinae includes the following genera: *Euomphaloceras* Spath, *Kanabiceras* Reeside & Weymouth, *Kamerunoceras* Reyment, *Schindewolfites* Wiedemann, *Romaniceras* Spath, *Yubariceras* Matsumoto, Saito & Fukada, *Shuparoceras* Matsumoto and *Obiraceras* Matsumoto. Also tentatively included here is the Lower? Cenomanian *Tunesites* Pervinquière.

The origins of the subfamily lie in the group of *Euomphaloceras cunningtoni* (Sharpe) which was derived from depressed and spinose *Acanthoceras rhotomagense* (Brongniart) during *Turrilites costatus* Zone times, by a weakening of the flank ribs and the development of intercalated ventral ribs (Kennedy 1971). *Acanthoceras rhotomagense pseudeuomphalum* Thomel may be a passage form. *Euomphaloceras* s.s., i.e. *euomphalum* (Sharpe), arose from this stock during *pentagonum* Zone times by a further weakening of ribbing relative to tubercula-

tion, and the appearance of constrictions in the early and middle growth stages (it should be noted that the earliest growth stages of *E. cunningtoni* are unknown and it too may possess constrictions on the juvenile whorls). *Kanabiceras* first appears in the uppermost Cenomanian (*gracile* Zone), and is easily derived from *E. euomphalum* merely by a joining of the siphonal tubercles so as to form a serrated keel. Passage forms are known (Kennedy 1971).

During the Lower Turonian, *Kanabiceras* gave rise to *Schindewolfites* and *Kamerunoceras*. *Kamerunoceras* Reyment is known with certainty only from the Lower Turonian of Nigeria and the Cameroons. Reyment (1955) regarded it as a probable offshoot of the *Protacanthoceras* stock that produced *Mammites*, *Watinoceras* and *Benueites*. The inner whorls of *Kamerunoceras*, however, bear a low crenulated keel with shallow sulci on either side, which therefore link it rather to the uppermost Cenomanian *Kanabiceras*.

Schindewolfites Wiedmann (1959) includes evolute forms with constricted early whorls, irregular ornament, and prominent tuberculation. In maturity, this genus may develop a row of lateral tubercles in addition to the umbilical, upper and lower ventro-lateral, and siphonal tubercles. The inner whorls of this genus bear a close morphological resemblance to *Kanabiceras* and a close phyletic relationship seems probable. Thomel (1972: 158) considered *Acanthoceras vergonsense* Thomel as the probable ancestor of *Schindewolfites*; this appears wholly untenable since there is a considerable temporal gap of several ammonite zones between the last appearance of *Acanthoceras* and the first appearance of *Schindewolfites*. Matsumoto (1975) suggested that *Schindewolfites* might best be treated as a subgenus of *Yubariceras*.

Matsumoto *et al.* (1957) interpreted *Yubariceras* as a multituberculate derivative of *Acanthoceras* s.s. although, more recently, Matsumoto (1975) considered the origins of the group should be sought in what he termed '. . . a certain species group of *Euomphaloceras* as well as in a transitional form between *Acanthoceras* and *Euomphaloceras*'. It is difficult to derive *Yubariceras* from either *Acanthoceras* or *Euomphaloceras* s.s. since, as with *Schindewolfites*, there is a considerable time gap between the first appearance of *Yubariceras* and the last appearance of *Acanthoceras* or *Euomphaloceras* s.s. *Yubariceras* first appears in the Lower Turonian and, in common with *Kanabiceras*, is very evolute, with a depressed whorl section, multituberculate ornament, and it bears constrictions on the early whorls. It is thus in this latter taxon (or one of its early Turonian derivatives) that the ancestry of *Yubariceras* should be sought.

Matsumoto *et al.* (1957) considered *Romaniceras* as a multituberculate derivative from the group of *Calycoceras newboldi—spinosum*. These two groups are indeed superficially similar, although the resemblances are simply due to homoeomorphy since the *newboldi* group die out early in the Upper Cenomanian (*pentagonum* Zone) and *Romaniceras* does not appear until about the Middle Turonian. As noted by Matsumoto (1975), *Romaniceras* and *Yubariceras* are closely allied, and it seems more likely that the typically Middle to Upper Turonian *Romaniceras* was derived from an early form of *Yubariceras*.

Wiedmann (1959) erected the subgenus *Romaniceras* (*Proromaniceras*) for upper Lower Turonian forms allied to *Calycoceras orientale* (Kossmat). Yet again, the resemblance is merely one of homoeomorphy, and the author would follow Matsumoto (1975) in considering *Proromaniceras* as a synonym of *Romaniceras* s.s.

Shuparoceras is a Lower to Middle Turonian genus '. . . allied to the subgroup of *Calycoceras choffati* in various respects' (Matsumoto 1975: 110). The group of *Calycoceras choffati* (Kossmat) died out early in the Upper Cenomanian, and clearly did not provide the ancestor of *Shuparoceras*. Again, the constricted inner whorls, evolute form, and multituberculate ornament of this latter genus are typical of the *Euomphaloceras–Kanabiceras* lineage, and it is here that the ancestry of *Shuparoceras* should be sought.

Obiraceras is a late Turonian genus allied to both *Yubariceras* and *Schindewolfites*, and Matsumoto (1975) considers its derivation from the latter genus the most likely. From a morphological and stratigraphical point of view, this derivation is quite acceptable. The author does not agree with Matsumoto (1975) that the Turonian multituberculate acanthoceratids are polyphyletic. Indeed, they form a closely allied (if excessively split) and intimately related group which clearly have their origins in the late Cenomanian *Euomphaloceras–Kanabiceras* lineage.

Two other constricted acanthoceratid genera remain to be discussed. *Tunesites* Pervinquière (1907) was erected for evolute (umbilicus 30–39% of diameter) pyritic nuclei, with compressed whorl sections. The flanks bear slightly flexuous, prorsiradiate ribs ornamented by upper and lower ventro-lateral and siphonal tubercles, while there are three more or less prominent constrictions per whorl. Pervinquière (1907) gave the range of his genus as uppermost Albian–Cenomanian, whereas Wright (in Arkell *et al.* 1957) considers it as an exclusively Lower Cenomanian taxon. According to Pervinquière's (1907) original account, the holotype of *T. choffati* Pervinquière comes from beds yielding *Forbesiceras obtectum* (Sharpe), a typically Middle Cenomanian species (Kennedy 1971). In terms of acanthoceratid phylogeny, *Tunesites* shows advanced morphological features which are not compatible with an Upper Albian–Lower Cenomanian age and, as with some of Pervinquière's other stratigraphic data, the horizon is perhaps doubtful. Consequently, any attempt to fit *Tunesites* into a phylogenetic scheme must, at present, be speculative.

Hourcquiceras Collignon (1939) was erected as a subgenus of *Calycoceras* for forms characterized by the presence of prominent constrictions on the juvenile whorls, and was considered a possible synonym of *Tunesites* by Wright (in Arkell *et al.* 1957). The subgenus is of Middle or Upper Cenomanian age, and closely resembles *Calycoceras* (*Gentoniceras*) in maturity. Collignon's (1939) figures do not show obvious constrictions, only periodic more strongly developed flank ribs (an identical feature to that seen in juvenile *Gentoniceras*). As the writer has no material before him, further speculation is not possible, but he prefers to leave *Hourcquiceras* in the Mantelliceratinae.

Genus *Euomphaloceras* Spath, 1923

Type species *Ammonites euomphalus* Sharpe, 1855

1923 *Euomphaloceras* Spath
1931 *Kanabiceras* Reeside & Weymouth
1937 *Cunningtoniceras* Collignon

Discussion

According to Wright (in Arkell *et al.* 1957: L414), the genus *Kanabiceras* differed from *Euomphaloceras* 'in that paired tubercles on venter are oblique, not transverse, and siphonal tubercles now form a nodose keel'. *Kanabiceras* first appears in the uppermost Cenomanian and is easily derived from the earlier (*pentagonum* Zone) *Euomphaloceras euomphalum* (Sharpe) merely by a joining of the siphonal tubercles so as to form a serrated keel. Kennedy (1971: 90), however, records intermediates between the two forms while noting that a nodose keel may sometimes be present in *E. euomphalum* (Sharpe). Moreover, with the wide range of variation seen in the Angolan material of *Kanabiceras septemseriatum* (Cragin), and also admitted by other authors (Matsumoto 1959*b*), together with the variability shown by *E. euomphalum* (Wright 1963), the distinctions between the two genera blur. The differences are not herein regarded as of generic status, and consequently *Kanabiceras* is treated as a subgenus of *Euomphaloceras*. The genus *Euomphaloceras* now may be subdivided as follows:

E. (*Euomphaloceras*). Shell very evolute, inflated, with depressed whorl section; prominent umbilical and lower ventro-lateral tubercles on some or all of main ribs. All ribs cross venter with small upper ventro-lateral and siphonal tubercles, more numerous than lower ventro-lateral tubercles. Inner and middle whorls with distinct constrictions in some species. Age: Middle–Upper Cenomanian.

E. (*Kanabiceras*). As for *E.* (*Euomphaloceras*) but with siphonal tubercles joining to form a prominent keel. Upper ventro-lateral tubercles more or less oblique to keel. Age: Upper Upper Cenomanian–Lower Turonian.

Subgenus *Kanabiceras* Reeside & Weymouth, 1931

Type species *Scaphites? septem-seriatus* Cragin, 1893

Euomphaloceras (*Kanabiceras*) *septem-seriatum* (Cragin, 1893)

Figs 4N–O, 10A–E, 12E–H, 18G–H
19G–L, 26A–B, 28

Scaphites? septem-seriatus Cragin, 1893: 240. Adkins 1928: 259.
Acanthoceras? kanabense Stanton, 1893: 181, pl. 36 (figs 6–8).
Acanthoceras kanabense Stanton, Moreman, 1927: 95, pl. 13 (fig. 5).
Kanabiceras kanabense (Stanton) Reeside & Weymouth, 1931: 12.
Neocardioceras septem-seriatum (Cragin) Moreman 1942: 213, pl. 33 (figs 11–12).
Prionotropis echinatus Douvillé, 1931: 34, pl. 3 (figs 1–5), pl. 4 (figs 1–3).
Neocardioceras (*echinatum*) (Douvillé) Spath, 1931: 316.

Kanabiceras septemseriatum (Cragin) Matsumoto, 1959*b*: 99, pl. 24 (fig. 1a–c). Powell 1963*a*: 316, pl. 31 (figs 9–10). Matsumoto *et al.*, 1969: 279, pl. 37 (figs 1–3). Cobban & Scott, 1972: 72, pl. 12 (figs 5–27).
Lyelliceras stanislausense Anderson, 1958: 247, pl. 8 (fig. 5).

Diagnosis

Shell very evolute (umbilicus 32–44% of diameter), inflated, with wide shallow umbilicus. Whorl section varies from almost quadrate to strongly depressed (W/H = 1,12–1,57). Ornament highly variable. Ribbing very weak to prominent, prorsiradiate, with prominent umbilical and lower ventro-lateral septate spines. Upper ventro-lateral spines or clavi more numerous than lower ventro-lateral spines. Ribbing projected strongly forwards on the venter so as to meet the serrated siphonal keel at an acute angle. The keel may be strongly serrated or only a row of weakly joined tubercles. On either side of the keel are sulci which may be very deep or almost non-existent. Intercalated ribs and striae of various strength are common on the flanks.

Description

This species is one of the most abundant members of the Salinas fauna and consequently the intra-specific variation can be more readily judged. The ornamentation of this species is highly variable. All the specimens have their recrystallized shell preserved.

The shell is very evolute, the preceding whorl being covered to the lower ventro-lateral tubercles, with a generally depressed whorl section; polygonal costally but with a rounded intercostal section. The umbilicus is wide and shallow, the umbilical shoulder well rounded and occasionally impressed to accommodate the prominent, but irregularly developed, lower ventro-lateral spines of the preceding whorl.

The ribbing of this species is highly variable; in some examples the ribbing dominates the ornament (Fig. 4F–G) whereas in others ribbing is subordinate and spines predominate (Fig. 10B–C). There is a morphological gradation of specimens between these two end members.

In SAM–PCA2761 (Fig. 12E–F) ribs arise at the umbilical seam and are faintly rursiradiate to the umbilical bullae, which are most strongly developed on the earlier whorls. From these bullae the ribs pass forward (prorsiradiate) to the lower ventro-lateral tubercles, which are again very irregularly developed. On the earlier whorls they seem to have been, almost invariably, obliquely clavate, but as diameter increases they become swollen and rounded and many form the bases of long septate spines, although not every tubercle developed into a spine. From these lower ventro-lateral tubercles the ribs flex strongly forwards to join prominent upper ventro-lateral clavi close to the siphonal line. There are far more upper ventro-lateral clavi than lower ventro-lateral tubercles. The upper ventro-lateral clavi are separated from the serrated keel by prominent sulci across which the ribbing is very weakly developed. There are more serrations to

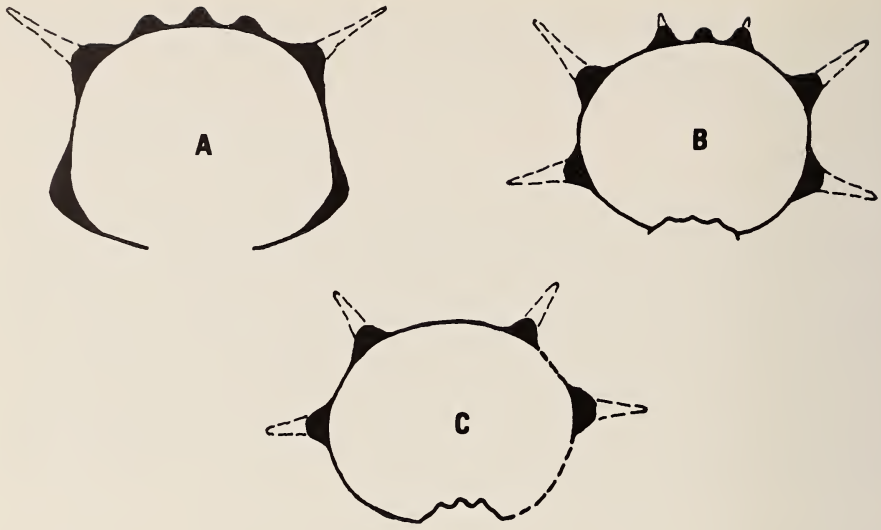

Fig. 28. *Euomphaloceras* (*Kanabiceras*) *septemseriatum* (Cragin). × 1. Whorl sections. A. SAM–PCA2736. B. SAM–PCA2810. C. SAM–PCA2742. × 1.

the keel than upper ventro-lateral clavi. Fine ribs and growth striae may be intercalated between main ribs. In this example tuberculation forms a subordinate part of the ornament. The greatest width is at mid-flank.

In SAM–PCA2835 (Fig. 12G–H) tuberculation is again very poorly developed, whilst there are only about seven major ribs per half whorl. Between these, however, are numerous thread-like, flexuous lirae, all of which bear upper ventro-lateral clavi, but rarely lower ventro-lateral tubercles.

The inner whorls of SAM–PCA2876 are very similar to the preceding example, but on the outer whorl the fine ribbing is virtually lost and it becomes even more coarsely ribbed than SAM–PCA2761. SAM–PCA2279 shows a further stage of development towards the effacement of ribbing. The major ribs are very distant, with only a few intercalated ribs, whilst the former have very prominent umbilical bullae, lower ventro-lateral tubercles and upper ventro-lateral clavi. The sulci separating the keel are very deep.

SAM–PCA2797 (Figs 10B–C) is an extreme individual in which virtually all ribbing is lost and tubercles dominate the ornament. Weak, prorsiradiate ribbing is evident to about 10 mm diameter, with short spines already impressed in the succeeding whorl. The ribbing, however, is far coarser at this stage than at later growth stages of many other examples, i.e. SAM–PCA2827 (Fig. 26A–B). Beyond this growth stage ribbing is effaced entirely and the ornament comprises occasional, very irregularly developed, umbilical bullae, of which there are 5 on the outer whorl, equally irregular lower ventro-lateral tubercles of which there are 13 on the outer whorl, 7 of which represent the bases of long, septate spines which pointed diagonally outwards. These are preserved impressed in the penulti-

mate whorl where they attain a length of 5 mm at only 10 mm diameter. The upper ventro-lateral clavi are more distant than in the other specimens, but still far outnumber their lower counterparts. The ventral sulci are weakly developed, forming two shallow grooves on either side of the keel. The serrated keel is formed by the joining together of the asymmetrical siphonal tubercles which are steepest adapically.

SAM–PCA2826 (Fig. 18G–H) is very similar to the previous example but differs in the extreme depression of the whorl section.

A probable pathological example is SAM–PCA2742 (Fig. 19K–L) which, up to a diameter of 35 mm, shows all the typical characters of this species. Immediately beyond this diameter, without any transitional stage, all ribbing and much of the tuberculation is entirely lost. The upper ventro-lateral clavi, the ventral sulci and the siphonal keel are all lost, leaving a smooth, broad, slightly convex venter. All ribbing on the flanks is lost, save fine growth lines, and the ornament comprises paired umbilical tubercles, which have now moved up to mid-flank, and ventro-lateral spines.

In another specimen, SAM–PCA2738, at about the same growth stage as the previous example, all the typical *Kanabiceras* features are retained. SAM–PCA2736 differs from the other specimens from these beds in having its greatest width at the umbilical shoulder. In this specimen the upper ventro-lateral clavi have become very irregular, with some representing swollen spine bases, whilst others have been suppressed to fine rib proportions. The ventral sulci are absent and the serrated keel has broken up into a row of irregular tubercles.

Measurements

No.	D	H	Wi	Wi/H	Uo	Ui
SAM–PCA2797	40	16 (40)	19 (48)	1,18	19	14 (35)
,,	20	9 (45)	11 (55)	1,22	9	8 (40)
SAM–PCA2827	50	18 (36)	25 (50)	1,39	26	18 (36)
,,	28	11 (39)	14 (50)	1,27	15	12 (43)
SAM–PCA2738	46	19 (41)	26 (56)	1,36	25	16 (35)
,,	40	16 (40)	18 (45)	1,12	?	14 (35)
SAM–PCA2811	25	9 (36)	12 (48)	1,33	13	10 (40)
SAM–PCA2835	22	9 (41)	12 (55)	1,33	?	7 (32)
SAM–PCA2761	31	12 (39)	15 (48)	1,25	18	10 (32)
,,	16	7 (44)	9 (56)	1,29	10	7 (44)
SAM–PCA2785	22	7 (32)	11 (50)	1,57	?	8 (36)
,,	18	6 (33)	8 (44)	1,33	8	6 (33)
SAM–PCA2742	51	17 (33)	19 (37)	1,12	?	?
,,	37	14 (38)	17 (46)	1,22	?	13 (35)
SAM–PCA2756	?	13	15	1,15	?	?
SAM–PCA2826	?	12	17	1,42	?	?
SAM–PCA2829	18	8 (44)	11 (61)	1,37	?	?

Discussion

As noted by previous authors (Matsumoto 1959*b*; Powell 1963), this is a highly variable species in which no two specimens are alike. The whorl section varies from almost quadrate to strongly depressed. Ribbing may be dominant to almost absent. Tuberculation may be very weak to extremely pronounced. The ventral sulci may be very deep to almost absent. The serrated siphonal keel is the most persistent character but it too may sometimes be represented by only a weakly connected row of siphonal tubercles. In a single (pathological?) specimen it is entirely lost.

Matsumoto (1959*b*) and Cobban & Scott (1972) have already shown that the American species *Kanabiceras kanabense* (Stanton) and *Lyelliceras stanislausense* Anderson do not bear separation from *K. septemseriatum*. The present study also confirms *Prionotropis echinatus* Douvillé to be a junior subjective synonym of *K. septemseriatum*.

Kanabiceras wyomingense Reeside & Weymouth (1931: 12, pl. 1 (fig. 14)) is a crushed *Neogastroplites cornutum* (Whiteaves) (Reeside & Cobban 1960: 67).

The Lower Turonian *Kanabiceras puebloense* Cobban & Scott (1972: 73, pl. 15 (figs 8–9), pl. 37 (figs 1–8), pl. 38 (fig. 1)) differs from *K. septemseriatum* in having more prominent uniform ribbing which, on the outer whorls at least, dominates the sculpture. It may be a *Kamerunoceras*.

The *Kanabiceras* sp. of Freund & Raab (1969: 9, pl. 1 (figs 3–6)) may or may not belong to this genus. The figured specimens are preserved as internal moulds and show prominent constrictions. In view of the range of variation shown by *E.* (*K.*) *septemseriatum*, together with the fact that the Israeli material comes from more or less the same stratigraphical level, they might be conspecific. Alternatively, they might possibly belong to *Euomphaloceras* s.s. or even represent juveniles of *Schindewolfites* or *Kamerunoceras*.

Occurrence

Euomphaloceras (*Kanabiceras*) *septemseriatum* (Cragin) is a widespread species, diagnostic of uppermost Cenomanian strata, and recorded from North America (Texas, Colorado, Montana, Kansas, Mexico, Utah, Arizona, California), Japan, Angola, Nigeria, France and England.

Subfamily Metoicoceratinae Hyatt, 1903
Genus *Metoicoceras* Hyatt, 1903
Type species *Ammonites swallovi* Shumard, 1861

Discussion

Metoicoceras is a typically uppermost Cenomanian genus (Kennedy & Juignet 1973), derived from the slightly earlier *Thomelites* (Wright & Kennedy in Juignet *et al.* 1973), and giving rise to the Lower Turonian *Jeanrogericeras*. *Jeanrogericeras* in turn gave rise to the middle and upper Turonian *Spathites* from which was derived (according to C. W. Wright, *in litt.*) the lower Coniacian

Buchiceras. From the host of species described, the majority of which have until now been regarded as endemic, there can be little doubt that species populations show a wide range of morphological variation, and that former narrowly defined species limits will break down when large collections are studied.

At present, *Metoicoceras* is known abundantly from the Western Interior of North America (Shumard 1861; Hyatt 1903; Moreman 1927, 1942; Haas 1949; Cobban 1953; Stephenson 1955; Young 1957, 1958), from Europe (d'Orbigny 1842; Petrascheck 1902; Leriche 1905; de Grossouvre 1912; Karrenberg 1935), Israel (Avnimelech & Shoresh 1962), Nigeria (Reyment 1955), Angola (Douvillé

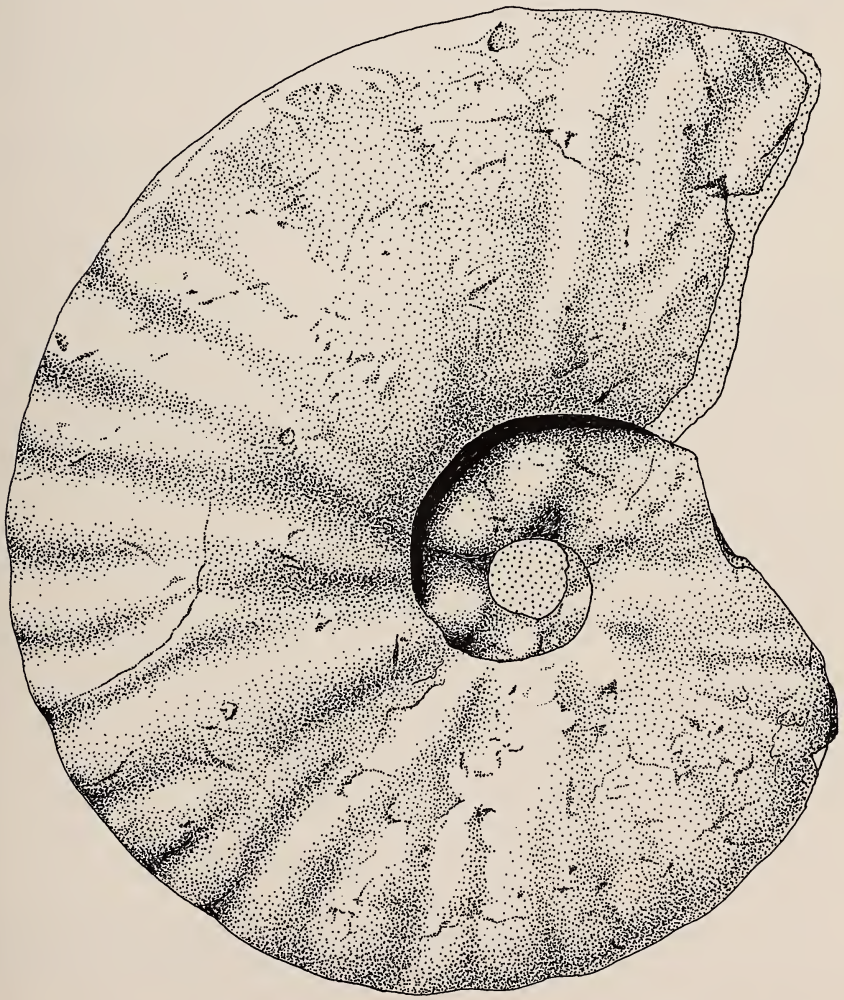

Fig. 29. *Metoicoceras geslinianum* (d'Orbigny). × 1. Lateral view of the crushed 'neotype', preserved as a composite internal mould. × 1.

1931; Cooper 1972, 1974), Morocco (Collignon 1963), Brazil (Reyment & Tait 1972*a*), and Madagascar (Collignon 1964).

In the Montana–Wyoming area of the Western Interior, Cobban (1953) recognized four levels of *Metoicoceras*:

M. whitei (youngest zone)
M. mosbyense
M. n. sp. (densely ribbed form)
M. praecox (oldest zone)

Of these four levels only the youngest, the level of *M. whitei*, corresponds to the *Sciponoceras gracile* Zone. It seems likely therefore, that *Metoicoceras* first appears at a somewhat earlier level in the Upper Cenomanian of North America than elsewhere, and that this region acted as an evolutionary pool prior to the somewhat later world-wide dispersal of the genus, a dispersal probably related to the late Cenomanian eustatic transgression (Cooper 1974).

As herein interpreted, the Metoicoceratinae includes the following genera: *Thomelites*, *Metoicoceras*, *Jeanrogericeras*, *Spathites* and *Buchiceras*.

Metoicoceras gibbosum Hyatt, 1903

Figs 21A–C, 30

Metoicoceras gibbosum Hyatt, 1903: 121, pl. 15 (figs 5–8). Moreman, 1927: 96, pl. 14 (fig. 4). Adkins, 1928: 248. Moreman, 1942: 211.
Mammites gibbosum (Hyatt) de Grossouvre, 1912: 25.
Buchiceras swallovi (Shumard) White, 1876: 202, pl. 20 (fig. 1a–c). Stanton 1893: 168, pl. 37 (fig. 1), pl. 38 (figs 1–3). Hill, 1901: pl. 40 (fig. 2).
Metoicoceras whitei Hyatt, 1903: 122, pl. 13 (figs 3–5), pl. 14 (figs 1–10, 15). Grabau & Shimer, 1910: 197, text-fig. 1457c–e. Moreman, 1927: 94, pl. 15 (fig. 1). Adkins, 1928: 249, pl. 26 (figs 1–2). Moreman, 1942: 210. Shimer & Shrock, 1944: 591, pl. 245 (figs 8–10). Cobban & Scott, 1972: 74, pl. 14 (figs 3–4, 9–11), pl. 16 (figs 1–2), text-fig. 34.
Metoicoceras kanabense Hyatt, 1903: pl. 15 (figs 9–11).
Mammites kanabensis (Hyatt) de Grossouvre, 1912: 24.
Metoicoceras acceleratum Hyatt, 1903: 127, pl. 14 (figs 11–14). Adkins, 1928: 249.
Mammites acceleratum (Hyatt) de Grossouvre, 1912: 25.
Metoicoceras ornatum Moreman, 1942: 211, pl. 32 (fig. 4).
Metoicoceras aff. *ornatum* Moreman, Reyment, 1955: 47, pl. 9 (figs 6–7). Collignon 1963: 34, pl. 19 (figs 1–2).
Metoicoceras aff. *mosbyense* Cobban, Collignon, 1963: 35, pl. 19 (fig. 3).
Metoicoceras cf. *whitei* Hyatt, Cooper, 1972: 248; 1974: 82, 86.
? Metoicoceras aff. *whitei* Hyatt, Böse, 1918: 203, pl. 12 (figs 4–7).
Pulchellia caicedoi Douvillé (*non* Karsten), 1931: 26, pl. 2 (fig. 1a–b).
? Metoicoceras besairei Collignon, 1964: 149, figs 1628–1629.
Barroisiceras trinodosum Moreman, 1927: 212, pl. 33 (figs 1–2).
? Metoicoceras bösei Jones, 1938: 127, pl. 10 (figs 1–3).
? Metoicoceras swallovi macrum Stephenson, 1952: 209, pl. 51 (figs 4–7).

Description

Only one example of this genus was collected from Salinas, and it may now be added to the '*Pulchellia caicedoi*' described by Douvillé (1931), as the only two representatives of *Metoicoceras* from the Salinas beds.

The specimen is a wholly septate phragmocone with the recrystallized test preserved. It is very involute, compressed, with broad convex flanks converging

towards the very narrow venter (Fig. 30). On the flanks, initially straight, later slightly flexuous, ribs arise at the umbilicus from very weak umbilical bullae and broaden markedly towards the venter. The ribbing on the inner portion of the flanks, closest to the umbilicus, is very faint and indistinct on the adoral half of the outer whorl. Between all long ribs there are almost invariably 1–2 ribs intercalated at about mid-flank. At the venter there are about 30 ribs on the outer whorl, with rib terminations broader than the interspaces. All ribs bear strong upper and weak lower ventro-lateral clavi, the latter weakening noticeably with age. Broad low ribs connect the upper ventro-lateral tubercles across the venter on the adoral portion of the outer whorl. The narrow venter is distinctly concave on the adapical portion of the outer whorl, but as tuberculation weakens it becomes tabulate. The greatest width is at mid-flank.

Measurements

No.	D	H	W	H/W	U
SAM–PCA2714	84	51 (61)	29 (35)	1,76	7 (8,3)
„	57	28 (49)	20 (35)	1,40	?

Discussion

The following ontogenetic features are apparent in the Angolan example before the writer: the shell becomes more compressed with age, the tuberculation weakens (especially the lower ventro-lateral clavi) considerably, the venter is showing the tendency, so typical amongst described forms, to round with

Fig. 30. *Metoicoceras gibbosum* Hyatt, SAM–PCA2714. Whorl section. × 1.

maturity, and flank ribbing weakens and becomes flexuous.

A score of 'species' have been described from western Europe and the Western Interior of North America. Casts of much of the North American type material, as well as photographs of the European types, kindly shown to the writer by W. J. Kennedy, leave no doubt whatsoever that the species of this genus are highly variable, and that the majority of described forms are merely nominal species.

Metoicoceras whitei Hyatt (1903: 122, pl. 13 (figs 3–5), pl. 14 (figs 1–10, 15)) was erected for one of Shumard's (1861) syntypes of *Ammonites swallovi* (Stephenson 1952), the types of which are now lost. Hyatt's (1903, pl. 13 (figs 3–5)) paratype still remains (USNM 29408) and shows the following features: shell compressed, involute on the inner whorls, with weak, but distinct, umbilical bullae giving rise to prorsiradiate ribs which broaden ventrally. There are about 9 such umbilical bullae (and main ribs) at a diameter of about 85 mm. Between main ribs there are generally 2 intercalatories. All ribs are ornamented with upper and lower ventro-lateral tubercles. On the body chamber, tuberculation weakens considerably, the venter rounds, the umbilical bullae are lost, and ribbing coarsens so that there is only a single intercalatory between main ribs. There are 30 ribs on the outer whorl.

Metoicoceras gibbosum Hyatt (1903: 121, pl. 15 (figs 5–8)) was founded on a single specimen differing from *M. whitei* only in being slightly more inflated, apparently lacking umbilical bullae and in having fewer (25) ribs on the outer whorl. Cobban & Scott (1972) regarded *M. gibbosum* and *M. whitei* as conspecific, placing the former into the synonymy of the latter. The writer concurs with these authors in regarding *M. whitei* and *M. gibbosum* as synonyms. However, contrary to Cobban & Scott (1972), the name *gibbosum* has page priority over *whitei*, and is thus the valid name.

Metoicoceras kanabense Hyatt (1903, pl. 15 (figs 9–11)) was figured but not described. It is a juvenile, strongly compressed and very involute, with about 28 prorsiradiate ribs on the outer whorl. Umbilical bullae are very weak or absent. All ribs are ornamented with upper ventro-lateral clavi, although lower ventro-lateral tuberculation appears to be absent. This species comes from the same horizon as *M. gibbosum* and is probably a synonym.

Metoicoceras acceleratum Hyatt (1903: 127, pl. 14 (figs 11–14)) is another species based on a juvenile. It is not, at present, directly comparable with the other species but, so far as can be judged from the photograph, is probably not distinct from *M. gibbosum*.

Stephenson (1952) has discussed *Metoicoceras swallovi* (Shumard); Shumard (1861) failed to illustrate his material, which is now lost. Stephenson (1952: 208) considered *M. swallovi* to show the following features: shell compressed, relatively evolute, with a moderately deep umbilicus; umbilical seam egresses markedly on the body chamber; outer whorl with 28 ribs, fewer on inner whorls, which are slightly prorsiradiate on the inner whorls but recurve on the body chamber so as to become convex adorally; at a diameter of about 60 mm there are 7 promi-

nent swollen umbilical tubercles per whorl which on the final whorl become more numerous and bullate; each tubercle gives rise to a single main rib, with 1–2 intercalatories on the inner whorls. Ribbing weakens towards the aperture; all ribs are ornamented with upper and lower ventro-lateral clavi, although the latter become obsolete on the body chamber; the narrow venter remains tabulate on the body chamber, while the upper ventro-lateral clavi remain strong throughout ontogeny.

Metoicoceras swallovi differs from *M. gibbosum* in being relatively more evolute, with more prominent, rounded umbilical tubercles, and in that the ribbing recurves on the body chamber. The strength of the umbilical tubercles has long been regarded as a diagnostic characteristic of many *Metoicoceras* species. So far as the writer is able to judge, this character is highly variable and its value in taxonomy has been overestimated.

Metoicoceras swallovi macrum Stephenson (1952: 209, pl. 51 (figs 4–7)) was said to differ from *M. swallovi* in being more compressed and with bullate umbilical tubercles in the early growth stages. This subspecies would seem merely to point to transitional forms between *M. gibbosum* and *M. swallovi.*

Metoicoceras mosbyense Cobban (1953: 48, pl. 6 (figs 1–14), pl. 7 (figs 1–3)) is a large species (? macroconch), very involute on the inner whorls but becoming rather evolute at large diameters. The inner whorls show prominent umbilical bullae, about 10 per whorl, giving rise to slightly prorsiradiate ribs, between which are 1–2 intercalatories. At the venter, at about 40 mm diameter, there are about 30 ribs per whorl. All ribs are ornamented with upper and lower ventro-lateral tubercles up to a diameter of 45 mm when the lower ventro-lateral tubercles become obsolete. At about 110 mm diameter the upper ventro-lateral clavi are lost and the venter becomes rounded. Also at this stage the ribs coarsen and become more robust, numbering only about 24 per whorl. This species was distinguished from *M. whitei* (= *M. gibbosum*) in its loss of lower ventro-lateral tubercles at small diameters.

Metoicoceras muelleri Cobban (1953: 49, pl. 6 (figs 15–16), pl. 8 (figs 1–7), pl. 9) is a compressed species with about 32 sigmoidal ribs per whorl at small growth stages, but ribbing coarsens on the outer whorl when there may only be 20. The lower ventro-lateral tubercles are lost at only 11 mm diameter. Cobban (1953) noted transitions between this species and the contemporaneous *M. mosbyense*, suggesting that the differences are not specific. The large size attained by *M. mosbyense* suggests that the differences might be sexual.

Metoicoceras defordi Young (1957: 1169, pl. 149 (figs 1–8), text-fig. 1a, e, g, i) is a compressed species, very involute on the inner whorls but becoming rather evolute on the outer whorls as the umbilical seam egresses. There are about 30 prorsiradiate ribs per whorl at 70 mm diameter, of which about one-quarter are long ribs ornamented with prominent umbilical bullae. There are generally 2 intercalatories between main ribs. The venter remains concave until about 100 mm diameter, after which it becomes tabulate, finally becoming rounded at diameters of about 150 mm. According to Young (1957: 1171)

'*Metoicoceras defordi*, n. sp., in whorl section and ornamentation appears to be related to *M. whitei* Hyatt, but the species is older than *M. whitei*, and the earlier disappearance of one pair of shoulder nodes and especially the flat topped ribs in the penultimate whorls and on the body whorls serve to separate the two species. The flat-topped ribs would appear to be a specific specialization not transmitted to any younger known species of the genus.'

Metoicoceras irwini Moreman (1927: 92, pl. 13 (figs 3–4)) is a compressed, very involute species with about 32 prorsiradiate ribs, broadening ventrally on the outer whorl, half of which is body chamber. Prior to the start of the body chamber all ribs are ornamented with weak lower ventro-lateral tubercles and prominent upper ventro-lateral clavi. On the adapical half of the outer whorl the venter is tabulate, presumably becoming rounded on the body chamber. The inner parts of the flanks are almost smooth and appear to be lacking in ornament. On the early parts of the body chamber the ribs are distinctly convex towards the aperture, but they straighten out adorally. This species is almost identical to *M. dumasi* (Pervinquière) which is probably not separable from *M. geslinianum*.

Metoicoceras boesei Jones (1938: 127, pl. 10 (figs 1–3)) is based on a poorly preserved holotype which shows the following features: shell compressed, relatively evolute. Fairly prominent umbilical bullae gives rise to one, rarely two, prorsiradiate main ribs which broaden ventrally. There are 2–3 intercalatories between main ribs. All ribs are ornamented with weak upper and lower ventro-lateral clavi. Ribs pass weakly across the narrow, tabulate venter. There were probably about 28 ribs on the outer whorl. This species differs from *M. gibbosum* and the Angolan example only in being more evolute.

Metoicoceras ornatum Moreman (1942: 211, pl. 32 (fig. 4)) is a compressed species, involute on the inner whorls but becoming rather evolute as the umbilical seam egresses. Long ribs arise from rather prominent umbilical bullae and are separated by 1–2 intercalatories. There are 21 ribs on the outer whorl, all of which broaden ventrally and are ornamented with prominent upper and lower ventro-lateral clavi to large growth stages. In the paratype, the ribbing becomes very coarse on the body chamber and forms prominent folds across the venter. This species occurs side by side with *M. whitei* (Moreman 1927: 93) (= *M. gibbosum*) and the writer does not regard the differences as of specific status.

'*Barroisiceras*' *trinodosum* Moreman (1927: 212, pl. 33 (figs 1–2)) is considered by Cobban & Scott (1972: 63) to be a pathological example of *M. whitei*. '*Barroisiceras*' *brittonense* Moreman (1927: 212, pl. 33 (fig. 3)) is possibly also a pathological *Metoicoceras*.

Metoicoceras latoventer Stephenson (1952: 209, pl. 51 (figs 4–7)) is an involute, compressed form in which the umbilical seam egresses markedly on the outer whorl. The final whorl bears 19 slightly sinuous, prorsiradiate ribs generally alternating long and short. Long ribs (13 to 15 per whorl) bear prominent conical umbilical tubercles up to 25 mm diameter, whereafter they become bullate. On the inner whorls all ribs are ornamented with lower ventro-lateral tubercles and upper ventro-lateral clavi, which become obsolete on the body chamber. Up to

about 25 mm diameter the juvenile shell shows a weak row of siphonal clavi. This species differs from *M. gibbosum* in being more evolute, with more numerous umbilical bullae and coarser, more distant flank ribbing.

Metoicoceras crassicostae Stephenson (1952: 210, pl. 58 (figs 6–8)) was based on a single specimen showing the following features: shell moderately inflated and rather evolute, with umbilical seam egressing markedly on the outer whorl; there are about 11 long ribs on the outer whorl which arise from prominent umbilical bullae; there are sporadic intercalatories between long ribs, with about 18 ribs on the outer whorl; the venter is 'considerably worn', but shows signs of upper and lower ventro-lateral tubercles. Stephenson (1952: 210) distinguished *M. crassicostae* from *M. latoventer* in that 'the venter of this species is broader and not quite so flat at a corresponding stage of growth, the ribs are fewer, the nodes on the umbilical shoulder are much stronger, and the nodes on and near the ventral angles are weaker'. So far as can be judged, *M. crassicostae* differs from *M. latoventer* in having fewer, more robust umbilical bullae on the inner whorls. It is thus close to *M. swallovi*, differing only in its more distant ribbing.

The North American species of *Metoicoceras* are at present difficult to evaluate, since they occur at different stratigraphic horizons and the population structures appear to differ with time. Thus while the inner whorls of *M. defordi* are very similar to *M. whitei*, Cobban & Scott (1972) consider Young's slightly older species to be distinctive. *Metoicoceras whitei* is itself very close to *M. geslinianum*, in fact it is doubtful whether the juvenile whorls can be distinguished. Until the American populations are objectively revised and compared with European material the writer prefers to refer the Angolan material to *Metoicoceras gibbosum*.

'*Metoicoceras*' *antiquum* (Karrenberg 1935: 139, pl. 31 (fig. 13)) does not appear to belong to this genus nor indeed the Metoicoceratinae. It is a Lower Cenomanian species better referred to the Mantelliceratinae.

Metoicoceras bethlehemense (Avnimelech & Shoresh) (1962: 533, pl. 15 (fig. 3)) is a strongly compressed (crushed ?) form with prorsiradiate ribs throughout ontogeny. Main ribs arise singly or in pairs from fairly prominent umbilical bullae, with 1–2 intercalatories between long ribs. On the inner whorls the flank ribs are distinctly flexuous. Upper ventro-lateral clavi are retained to maturity, although the lower ventro-lateral tubercles are lost on the body chamber. This species is doubtfully separable from *M. gibbosum*.

Ammonites geslinianus d'Orbigny (1850: 146) (Fig. 29) was proposed for *Ammonites catillus* d'Orbigny (*non* Sowerby) (1840: 325, pl. 97 (figs 1–2)) from the uppermost Cenomanian of Lamnay, Sarthe. D'Orbigny's synthetograph, highly idealized as was frequently the case, shows a very compressed form, very involute (although the umbilical seam egresses markedly on the final whorl), and with flexuous ribs (about 30 per whorl) broadening rapidly towards the venter. Ribs arise singly or in pairs from fairly distinct umbilical bullae, with 1–2 intercalatories between main ribs. On the final whorl all ribs are ornamented with

upper ventro-lateral clavi only, the lower ventro-lateral tubercles having become obsolete at an early growth stage. Sornay (1955, fiche 11, figs 3–4) refigured d'Orbigny's example, showing the ribbing to become very slightly convex adorally on the body chamber, at which stage, also, the venter becomes rounded. This adorally convex ribbing is well shown by *Metoicoceras pontieri* Leriche (1905: 120, pl. 2) which Wright & Kennedy (in Juignet *et al.* 1973) consider a junior subjective synonym of *M. geslinianum*.

Metoicoceras geslinianum (d'Orbigny) appears to differ from *M. gibbosum* and the Angolan example, only in losing its lower ventro-lateral tubercles at small sizes, and in the recurvature of the flanks ribs on the body chamber. Wright & Kennedy (in Juignet *et al.* 1973) considered *Metoicoceras petraschecki* (de Grossouvre) (1912: 22, pl. 2 (fig. 2)), *M. bureaui* (de Grossouvre) (1912: 22, pl. 1 (fig. 2)) and *M. dumasi* (de Grossouvre) (1912: 23, pl. 2 (fig. 1)) as probable synonyms of *M. geslinianum*.

Metoicoceras gourdoni (de Grossouvre) (1912: 20, pl. 1 (fig. 1)) is a relatively evolute species with 6 prominent umbilical bullae on the penultimate whorl, from which arise coarse, robust, almost rectiradiate ribs which broaden ventrally. On the adoral portion of the outer whorl the ribbing becomes convex adorally. There is a single intercalatory between main ribs on the outer whorl, with 21 ribs per whorl. Unless there are two or more intercalatories between main ribs on the inner whorls, which seems likely, juveniles are equally distantly ribbed. At the largest growth size, which includes about a half-whorl of body chamber, there are prominent upper and lower ventro-lateral tubercles. The most distinctive features of *M. gourdoni* are, therefore, its relatively evolute form, distant, robust ribbing and the persistence of the ventro-lateral tubercles to large diameters. These features serve to distinguish the holotype from *M. geslinianum*.

Metoicoceras stoliczkai Sastry & Matsumoto (1967: 2, pl. 1 (fig. 1)) from the topmost beds of the Utatur Group of southern India differs from all other *Metoicoceras* species in having a deep, crater-like umbilicus, with steep umbilical walls. This feature, together with the suture-line, suggests it is better referred to the Lower Turonian *Jeanrogericeras*. Indeed, it would appear to be conspecific with *J. binicostatum* (Petrascheck) (cf. Wiedmann 1964: 126, figs 10–11).

Collignon (1964) described a number of species of *Metoicoceras*, supposedly from the 'Lower' Cenomanian of Madagascar. Almost all the typical Upper Cenomanian species recorded from Madagascar are reported from this 'Zone à *Mantelliceras mantelli* et *Calycoceras newboldi*', and leave little doubt that the faunas of this zone represent collecting from different palaeontological horizons. However, it is difficult to ascertain whether they represent true *Metoicoceras* or are homoeomorphous mantelliceratinids allied to *Utaturiceras* and *Graysonites*.

Metoicoceras swalloviforme Collignon (1964: 149, fig. 1627) is a moderately evolute species with about 11 fairly prominent umbilical bullae on the outer whorl, from which arise slightly prorsiradiate ribs. Between long ribs there is generally an intercalatory, so that there are 22 ribs on the outer whorl. All ribs are ornamented with small, pointed lower ventro-lateral tubercles and prominent

upper ventro-lateral clavi. This species was said to differ from *M. swallovi* in whorl section and details of the suture-line. As noted by Hyatt (1903), however, the suture-line is highly variable. The main difference from *M. swallovi* appears to be in the more robust, distant ribbing of *M. swalloviforme*, and in being somewhat more inflated. It is thus close to *M. crassicostae* Stephenson.

Metoicoceras besairiei Collignon (1964: 149, figs 1628–1629) is a compressed species with flat flanks, a very narrow umbilicus and a concave venter. Ornament comprises 10–12 long ribs, with weak umbilical bullae, between which are 1–2 intercalatories. The ribs are prorsiradiate, and number about 17 ribs per half whorl. All ribs are ornamented with lower ventro-lateral tubercles and upper ventro-lateral clavi. *Metoicoceras besairiei* was said to differ from *M. whitei* in having more flexous ribbing, maximum width near the umbilicus and in differences in the suture-line. The differences are slight.

Metoicoceras sakarahense Collignon (1964: 150, figs 1630–1632) shows the following features: the ribbing is very fine; main ribs are slightly more prominent than the intercalatories, and are slightly flexous, prorsiradiate, with weak umbilical bullae; between 2 and 4 intercalatories between main ribs; all ribs are ornamented with upper and lower ventro-lateral tubercles; on the adoral portion of the outer whorl, the ribbing forms a chevron across the venter; there are at least 42 ribs per whorl.

Metoicoceras fasciculatum Collignon (1964: 151, fig. 1633) was characterized by the sinuous, fasciculate nature of the ribbing. It is a small species, very involute, with flat, parallel flanks. There are about 23 very sinuous main ribs which arise at the umbilicus. Of these, some are simple while others give rise, at various levels on the flanks, to 2–3 secondaries, so that there are 40 ribs at the venter of the outer whorl. Umbilical tubercles appear to be lacking, although some of the ribs may be weakly flared near the umbilicus. All ribs are ornamented with upper and lower ventro-lateral tubercles. Ribbing forms a weak chevron across the venter.

Thus, of 27 described 'species' of *Metoicoceras*, two (*M. antiquum* Karrenberg and *M. stoliczkai* Sastry & Matsumoto) do not belong to this genus, while *M. gibbosum* Hyatt includes amongst its synonyms *M. whitei* Hyatt, *M. kanabense* Hyatt, *M. acceleratum* Hyatt, *M. ornatum* Moreman and possibly also *M. boesei* Jones, *M. bethlehemense* (Avnimelech & Shoresh) and *M. besairiei* Collignon. *Metoicoceras muelleri* Cobban and *M. defordi* Young are possible synonyms of *M. mosbyense*, while probable synonyms of *M. geslinianum* include *M. pontieri* Leriche, *M. bureaui* (de Grossouvre), *M. petraschecki* (de Grossouvre), *M. dumasi* (de Grossouvre), *M. gourdoni* (de Grossouvre) and *M. irwini* Moreman. *Metoicoceras crassicostae* Stephenson and *M. latoventer* Stephenson are doubtfully separable contemporaneous species, while *M. swallovi* is not well known and its affinities are unclear. The difficulties associated with the Madagascan species have already been noted; *M. swalloviforme* appears to belong to the *swallovi-crassicostae* group, while *M. sakarahense* Collignon and *M. fasciculatum* Collignon are doubtfully separable.

Occurrence

Metoicoceras gibbosum is recorded from the uppermost Cenomanian of Texas, Mexico, the Western Interior, Morocco, Nigeria and Angola, and is possibly also present in the Middle East and Madagascar.

Subfamily Mammitinae Hyatt, 1900
Genus *Watinoceras* Warren, 1930

Type species *Watinoceras reesidei* Warren, 1930
(= *Acanthoceras amudariense* Arkhangel'skii, 1916)

1930 *Watinoceras* Warren
1954 *Benueites* Reyment

Discussion

As diagnosed by Wright (in Arkell *et al.* 1957: L416), *Watinoceras* shows the following features: 'Early whorls compressed, finely ribbed, with inner and outer ventro-lateral and siphonal tubercles as in *Neocardioceras*, but siphonal row soon lost; later, venter may be concave between rows of ventro-lateral clavi or rounded, with ribs passing over in chevrons; ornament usually coarsens with age.'

Wright's (in Arkell *et al.* 1957) diagnosis was based upon '*Acanthoceras*' *amudariense* Arkhangel'skii (1916: 48, pl. 7 (figs 8–13)) and undescribed forms from Devonshire said to be transitional from *Neocardioceras* to *Watinoceras* (cf. Reyment 1955: 55). Siphonal tubercles are not known in the holotype of *W. reesidei*, nor have they ever been recorded from undoubted species of this genus. Consequently, contrary to Reyment (1955), any forms possessing siphonal tubercles are best retained in the genus *Neocardioceras*, and *Watinoceras* is restricted for those species with a quadrituberculate venter at some or all growth stages.

On the basis of the North American material, Cobban & Scott (1972: 75) gave the following, somewhat contrasting diagnosis of *Watinoceras*: 'This is a moderately evolute genus that has somewhat compressed whorls, narrow but conspicuous ribs, and umbilical, lower ventro-lateral, and upper ventro-lateral tubercles of which the upper ventro-lateral ones are the strongest. The siphonal area is narrow, somewhat flattened, and bordered by the high closely spaced upper ventro-lateral tubercles. Ribs are prorsiradiate and, on the inner whorls, sigmoidal. The suture is rather simple and has a wide slightly incised first lateral saddle and much narrower lateral lobe.'

This conflicting diagnosis is due to the fact that Cobban & Scott (1972) based their diagnosis of *Watinoceras* on the apparently immature *W. reesidei* Warren and the adult *W. coloradoense* (Henderson), neither of which shows the change in ornament exhibited by *W. amudariense* (Arkhangel'skii).

Callomon (1963), in his important work on sexual dimorphism in ammonites, considered three features to be diagnostic of the attainment of maturity by an ammonite. These were:

(i) A change in the style of ornament.

(ii) Uncoiling of the umbilical seam.

(iii) Sutural approximation.

The inner whorls of *Watinoceras amudariense* (Arkhangel'skii) are ornamented with upper and lower ventro-lateral tubercles, between which the venter appears flattish. On the adoral half of the outer whorl, however, the ventro-lateral tuberculation is lost, the venter becomes rounded, and the ribs form prominent chevrons across the venter. Moreover, between 15 and 21 mm diameter *W. amudariense* has an umbilical ratio of 38,8–39,5 per cent, whereas at the adoral end of the outer whorl the umbilical ratio is 41,5 per cent. Arkhangel'skii's (1916) material would seem to retain recrystallized test, and hence the nature of the suture-line is unknown. The fact that *Watinoceras amudariense* shows two of the features considered diagnostic of maturity (Callomon 1963) is significant, and the writer regards *W. amudariense* as mature.

A number of authors (Reyment 1955; Collignon 1963; Cobban & Scott 1972) have regarded '*Acanthoceras*' *amudariense* var. *horridum* Arkhangel'skii (1916: 49, pl. 8 (figs 8–10, 14–15)) as conspecific with *Watinoceras coloradoense* (Henderson), an assignment with which the writer concurs. The latter species, however, attains diameters of 110 mm (Cobban & Scott 1972), and rather than lose tuberculation in maturity, the ventro-lateral tubercles become very pronounced, while ribbing coarsens. Cobban & Scott (1972) noted, however, that an impression of the inner whorls of the holotype of *W. coloradoense* (Fig. 27) 'shows strong narrow rectiradiate ribs numbering 15 per half whorl at a diameter of approximately 24 mm'. The inner whorls thus bear a close resemblance to both *W. amudariense* and *Watinoceras reesidei* Warren. It is thus significant that Cobban & Scott (1972) record *W. reesidei* from the same horizon as *W. coloradoense*.

Cobban & Scott (1972: 76) considered Warren's (1930, 1947) type and topotype material of *Watinoceras reesidei* to show the following features: '(The shells) are moderately evolute, and their umbilical ratio is about 40%. The whorls, which are higher than wide, are ornamented with numerous narrow slightly signoidal prorsiradiate ribs of which about every other one extends to the umbilicus. Each rib bears a small sharp lower ventro-lateral tubercle and a slightly larger upper ventro-lateral tubercle. Most of the ribs that extend to the umbilicus have a low bullate umbilical tubercle. The last half whorl of the holotype has 22 ribs.'

These are the exact features which characterize *Watinoceras amudariense* (Arkhangel'skii), except that in the latter species tuberculation is lost at diameters of the order of 25 mm, whereafter the ribs form chevrons across the venter. Since none of Warren's (1930, 1947) material is over 20 mm in diameter the differences

are not considered significant, and *Watinoceras reesidei* Warren is considered a junior subjective synonym of *W. amudariense* (Arkhangel'skii).

The interesting situation is now arrived at that the small *Watinoceras amudariense* occurs side by side with the large *Watinoceras coloradoense* from areas as far afield as Alaska (Cobban & Gryc 1961), Alberta (Warren 1930), Colorado (Cobban & Scott 1972), Turkestan (Arkhangel'skii 1916) and possibly Morocco (Collignon 1966). As has already been noted, the inner whorls of *W. coloradoense* are finely ribbed and thus close to *W. amudariense*. Indeed, the rib density of *W. reesidei* and *W. amudariense* falls within the range of variation observed for juvenile *W. coloradoense* (Fig. 29), and it seems likely that at this growth stage the two species cannot be separated. The two species *W. amudariense* (Arkhangel'skii) and *W. coloradoense* (Henderson) thus show all the prerequisites of sexual dimorphism, viz. the inner whorls appear to be indistinguishable; they attain maturity at greatly differing diameters; the microconch shows a marked change of ornament on the body chamber and they occur side by side, and consequently are herein interpreted as microconch and macroconch respectively. The oldest available name is *W. coloradoense* (Henderson).

The genus *Benueites* Reyment is very close to *Watinoceras*, the main points of difference being that the former has a sulcate venter, finer ribbing and less regular tuberculation. The differences are merely ones of degrees, and are herein considered as of only subgeneric status. Of interest is the fact that Reyment (1971*b*) has recently recorded dimorphism within *Benueites*, dimorphs being separated on the basis that 'one of the pair is ornamented with dense ribs which are feebly adorned with tubercles, while the other member has much coarser ribbing, and usually three rows of tubercles, namely, umbilical, upper and lower ventro-lateral, the former being mostly more numerous and stronger than the umbilical row. The ventral furrow of the first group is deep and narrow and seldom cut by ribs, whereas that of the second category is broad and shallow and frequently crossed by ribs.' Whilst Reyment (1971*b*) considered this to be a novel type of dimorphism, it appears that the differences are largely due to a comparison of microconch dimorphs with the middle whorls of the corresponding macroconch. The genus may now be divided as follows:

W. (*Watinoceras*). Shell evolute, with prominent ribbing bearing umbilical and upper and lower ventro-lateral tubercles. Dimorphic; microconchs small with ventro-lateral tubercles lost on the body chamber, when the ribs form a chevron across the venter. Macroconch relatively large, tubercles and ribbing becoming coarser and more prominent with age.

Age: Basal Lower Turonian.

W. (*Benueites*). Similar to *W.* (*Watinoceras*), but microconch with very reduced tuberculation and a prominent siphonal sulcus across which ribbing is effaced. Macroconch with coarser ribbing and tuberculation and a weakly developed ventral sinus across which ribs are weakly connected. Age: Upper Lower Turonian.

Watinoceras (*Watinoceras*) *coloradoense* (Henderson, 1908) (♀)

Figs 18C–D, 19E–F, 31–34

Microconch (♂)

Acanthoceras amudariense Arkhangel'skii, 1916: 48, pl. 7 (figs 8–13).
Watinoceras reesidei Warren, 1930: 67, pl. 3 (fig. 2), pl. 4 (figs 9–12). Cobban & Gryc, 1961: 186, pl. 38 (figs 44–49). Hattin, 1965: text-fig. 3. Cobban & Scott, 1972: 75, pl. 27 (figs 7–10), pl. 28 (fig. 4).
? Watinoceras nov. sp. aff. *reesidei* Warren, Collignon, 1966: 37, pl. 19 (figs 14–15).
Sumitomoceras amudariense (Arkhangel'skii) Matsumoto *et al.*, 1969: 282.

Macroconch (♀)

Acanthoceras coloradoense Henderson 1908: 259, pl. 13, figs 10–11.
Acanthoceras amudariense var. *horridum* Arkhangel'skii, 1916: 49, pl. 8 (figs 8–10).
Gauthiericeras aff. *bravaisi* (d'Orbigny) Moreman, 1927: 96, pl. 14 (fig. 2).
Watinoceras coloradoense (Henderson) Reyment, 1955: 57; Collignon 1963: 37. Cobban & Scott, 1972: 76, pl. 27 (figs 11–19), pl. 28 (figs 1–3, 5–9).
? Watinoceras nov. sp. aff. *coloradoense* (Henderson) Collignon, 1966: 37, pl. 20 (figs 1–3).
Watinoceras horridum (Arkhangel'skii) Matsumoto *et al.*, 1969: 282.

Description

Two specimens, one beautifully preserved, the other rather crushed, appear to belong here. Both are entirely septate and have the recrystallized test preserved.

SAM–PCA2730 (Fig. 18C–D) is rather evolute, with about three-quarters of the penultimate whorl visible, and has a compressed whorl section, polygonal costally but rounded intercostally (Fig. 32). The flanks are slightly convex with maximum width at mid-flank. The umbilicus is moderately wide and rather deep, with a steep umbilical wall, slightly undercut at the umbilical seam. The umbilical shoulder is abruptly rounded.

At a diameter of 48 mm there are 41 ribs per whorl, with only 19 arising from bullae on the umbilical shoulder. These bullae are rather prominent to a diameter of 38 mm, after which they weaken considerably. Between each main rib there is invariably a shorter intercalated rib, occasionally two. Ribbing is strong and sharp, prorsiradiate across the flanks. Up to 25 mm diameter the ribs are rather rigid and straight, beyond which they become flexuous and convex forwards. At 38 mm diameter, when the umbilical bullae become obsolete, the main ribs are seen to continue across the umbilical wall to the umbilical seam. Ribs are narrowest near the umbilicus and broaden ventrally. At the lower ventro-lateral clavi the ribs bend forwards to the upper ventro-lateral clavi, crossing the venter with a slight adoral convexity. Siphonal tubercles are lacking at all visible growth stages. The ventro-lateral tubercles only become clavate at about the same stage as the umbilical tuberculation is lost (38 mm diameter). Prior to this, prominent bubble-like lower ventro-lateral tubercles occur only on the main ribs, while similar bubble-like upper ventro-lateral tubercles occur on all ribs. Up to 38 mm diameter the upper ventro-lateral tubercles are distinctly higher than the ribbing across the venter, so that the venter has a concave aspect. Beyond this

Fig. 31. *Watinoceras coloradoense* (Henderson). Lateral and ventral views of the holotype. Note fine ribbing of the inner whorls on the external mould. Photo: W. J. Kennedy. × 1.

Fig. 32. *Watinoceras coloradoense* (Henderson) (♀).
Whorl sections of SAM–PCA2730. × 1.

diameter, the upper ventro-lateral clavi are no higher than the ribbing, giving the venter a tabulate appearance. The suture-line (Fig. 33) closely resembles that of *Watinoceras coloradoense* (Henderson) as figured by Cobban & Scott (1972).

The shell of SAM–PCA2753 (Fig. 19E–F) is rather evolute, with a moderately wide umbilicus. The umbilical wall is steep and slightly undercut at the umbilical seam. The umbilical shoulder is well rounded with broad, flattish flanks.

Ornament comprises rather weakly developed umbilical bullae from which arise slightly prorsiradiate main ribs, separated by 1–2 intercalatories. There are 18 ribs per half whorl, generally with upper and lower ventro-lateral clavi. The

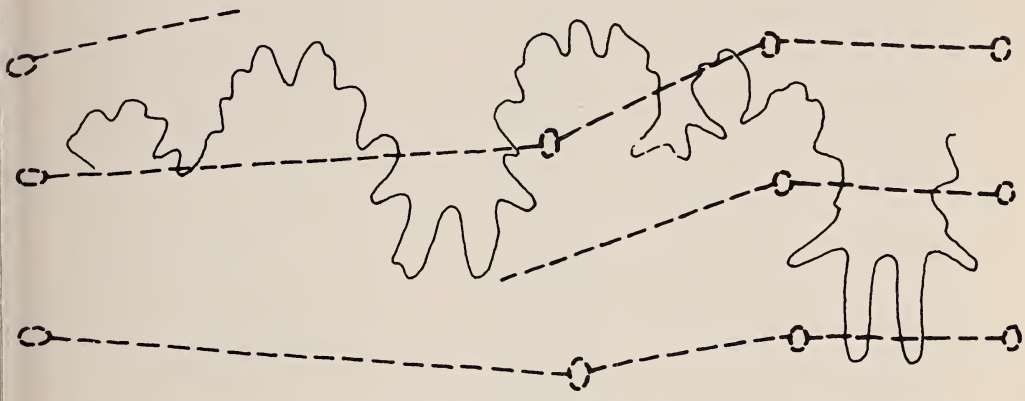

Fig. 33. *Watinoceras coloradoense* (Henderson) (♀). Suture-line of SAM–PCA2730 at about 48 mm diameter.

upper ventro-lateral clavi are very close together and stand out above the ribbing, giving the venter a concave aspect. There is no sign of siphonal tubercles at any stage.

Measurements

No.	D	H	W	W/H	U
SAM–PCA2730	48	21 (44)	17 (35)	0,81	15 (31)
,,	35	16 (46)	12 (34)	0,75	9 (26)
SAM–PCA2753	41	17 (41)	13 (31)	0,76	14 (34)

Discussion

As shown above, *Watinoceras coloradoense* (Henderson), *W. reesidei* Warren and *W. amudariense* (Arkhangel'skii) are conspecific, the oldest available name being *W. coloradoense*.

There appears to be a wide range of variation, both ontogenetic and intraspecific, within Henderson's species. The variation in rib density within the macroconch is well shown by Cobban & Scott (1972) (see also Fig. 34), while these authors record 1–3 intercalatories between main ribs in this species. Arkhangel'skii's (1916, pl. 8 (figs 8, 14)) juvenile macroconchs, however, show only simple, main ribs. Moreover, the diameter at which the coarse macroconch ornament first appears is also variable. Thus, typical '*Watinoceras coloradoense*-type' ornament appears at only 25 mm diameter in '*Acanthoceras*' *amudariense* var. *horridum*, whereas the Angolan example still retains '*Watinoceras reesidei*-type' ornament at 48 mm diameter. A similar amount of variation would also

seem to occur in the first appearance of adult ornament in the microconch. Thus, '*Acanthoceras*' *amudariense* is adult at 30 mm diameter, whereas Cobban & Scott (1972) note that 'impressions of *Watinoceras reesidei* from north-western Montana (Cobban, 1956*a*, p. 1003–1004) suggest that the adults attain diameters of 70–80 mm and that the adult whorls are about as densely ribbed as the juvenile whorls'. It seems likely, however, that some of the specimens interpreted by Cobban & Scott (1972) as juvenile *W. coloradoense* are in fact microconchs and, conversely, some of those interpreted as adult *W. reesidei* are merely densely ribbed, immature variants of the macroconch. Consequently, previous records of these species now need reinvestigation under this new light.

Matsumoto (in Matsumoto *et al.* 1969) assigned '*Acanthoceras*' *amudariense* to *Sumitomoceras*, a genus to which it most certainly does not belong. None the less, it is significant that the Angolan example closely resembles certain species of *Tarrantoceras* (= *Sumitomoceras*), e.g. *T. rotatile* Stephenson (Fig. 20). However, in *Tarrantoceras*, a siphonal row of tubercles persists to large diameters, and is only lost on the final whorl, while siphonal tubercles are unrecorded from undoubted *Watinoceras*.

Family **Vascoceratidae** Spath, 1925

Discussion

Wright (in Arkell *et al.* 1957: L418) gave the features of this family as: 'Derivatives of Acanthoceratinae which rapidly lose ribbing and tuberculation of that subfamily and are either smooth or bluntly tuberculate or have sparse coarse ribs. Suture may comprise shallow, irregular and slightly indented or deep and much indented elements. The whorl section and degree of involution is variable, even within species. Typically Tethyan in occurrence.'

Within the family Vascoceratidae, Wright (in Arkell *et al.* 1957) included the following genera: *Nigericeras*, *Spathites*, *Gombeoceras*, *Ezilloella*, *Paravascoceras*, *Pachyvascoceras*, *Vascoceras*, *Paramammites*, *Plesiovascoceras*, *Fagesia*, *Thomasites* and *Neoptychites*.

Wiedmann (1959) subdivided the family into two subfamilies, the Vascoceratinae and the Fallotitinae, based on the presence or absence of siphonal tubercles. The subfamily Fallotitinae, which lacks siphonal tubercles, was thought to be derived from the Mammitinae, while the Vascoceratinae, with siphonal tubercles, was considered to have evolved from the Acanthoceratinae. Within the Fallotitinae, Wiedmann (1964: 127) placed the genera *Plesiovascoceras*, *Fallotites*, *Paramammites*, *Ingridella*, *Spathitoides*, *Neoptychites* and doubtfully *Metasigaloceras*. This leaves *Nigericeras*, *Spathites*, *Gombeoceras*, *Ezilloella*, *Paravascoceras*, *Pachyvascoceras*, *Vascoceras*, *Fagesia* and *Thomasites* within the Vascoceratinae.

Of all the species of *Vascoceras* s.s. described by Choffat (1898), Pervinquière (1907), Reyment (1954*b*, 1955), Barber (1957), and Freund & Raab (1969), no mention is made of siphonal tubercles at any growth stage. Moreover, through the kindness of P.-Y. Berthou, the writer obtained excellent photographs

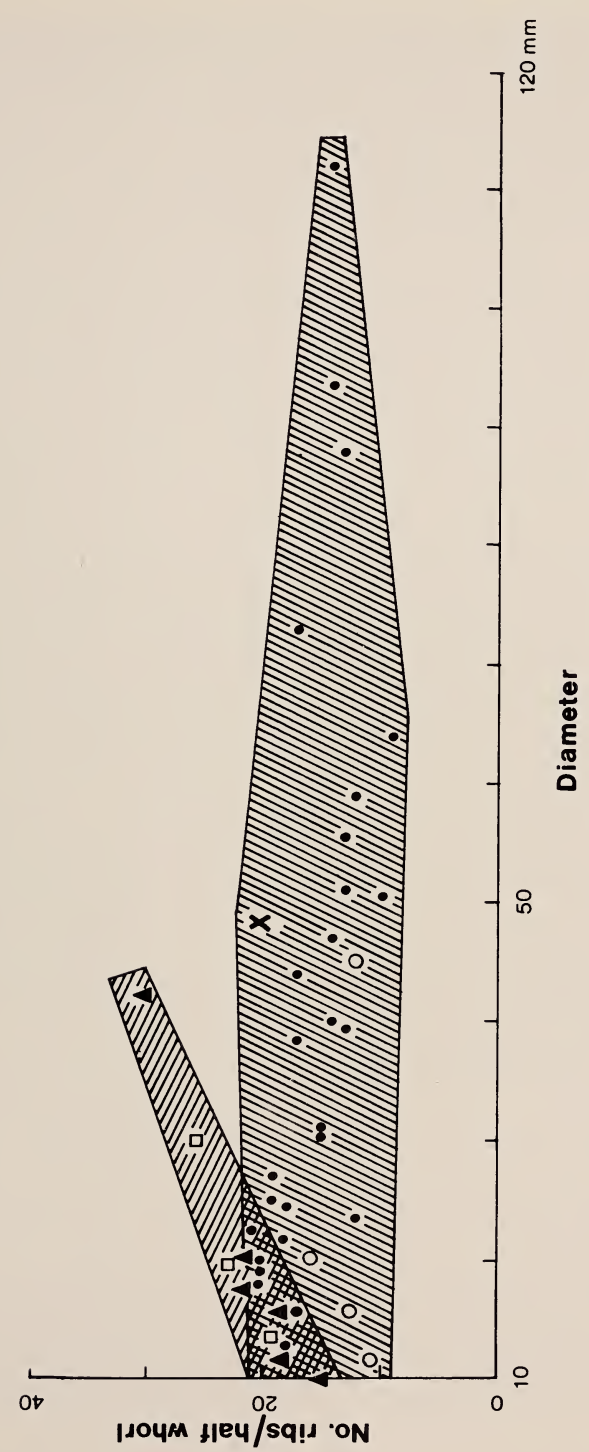

Fig. 34. Plot of rib density against diameter for specimens of *Watinoceras reesidei* Warren (triangles), *W. amudariense* (Arkhangel'ski) (squares), *W. amudariense* var. *horridum* (Arkhangel'ski) (circles), *W. coloradoense* (Henderson) (dots), and the Angolan example (cross). Data in part after Cobban & Scott (1972).

of all of Choffat's (1898) specimens, none of which shows siphonal tubercles. This is confirmed by an examination of the type material (P.-Y. Berthou, pers. comm.) and would appear to invalidate Wiedmann's subdivision of the family Vascoceratidae.

Genus *Vascoceras* Choffat, 1898

Type species *Vascoceras gamai* Choffat, 1898

The genus *Vascoceras* Choffat (type species *Vascoceras gamai* Choffat, 1898: 54, pl. 7, pl. 8 (fig. 1), pl. 10 (fig. 2), pl. 21) was diagnosed by Barber (1957: 13) as follows: 'Shell discoidal, or subglobose; whorls normally largely embracing. Venter sub-acute, rounded or flattened. Umbilicus steep sided. Early whorls ornamented with strong umbilical tubercles and fold-like costae which cross the venter. With age the ornament is lost and the last whorl is normally smooth. Suture line: three incised broad saddles and three bifid or denticulate lobes.'

The genus *Paravascoceras* Furon (type species *Vascoceras cauvini* Chudeau, 1909: 67, pls 1–3) was considered by Freund & Raab (1969) to include the synonyms *Pachyvascoceras* (Furon 1935: 58), *Paracanthoceras* (Furon 1935: 59), *Broggiiceras* (Benavides-Cacères 1956: 409) and *Discovascoceras* (Collignon 1957: 11). These authors diagnosed the genus as follows: 'Vascoceratids lacking umbilical tubercles. Compressed and involute at early stages; less involute later. During growth, there is either a short or a very long stage without any ornament. Lateral or marginal bulges sometimes appear; prorsiradiate ribs, uninterrupted crossing the venter, usually appear at a late stage. They rarely attain the umbilical border. The suture is simple and typical for the family.'

Freund & Raab (1969: 20) considered the most diagnostic feature of *Paravascoceras* to be the absence of umbilical tubercles at early growth stages.

Greenhornoceras (type species *Vascoceras* (*Greenhornoceras*) *birchbyi* Cobban & Scott 1972: 85, pl. 22, pl. 23 (figs 1–13), pl. 24 (figs 1–12), pl. 25, pl. 26 (figs 5–8, 11–12), pl. 27 (figs 1–6)) was erected as a subgenus of *Vascoceras* for those forms differing in being more involute and in maintaining a squarish or rectangular whorl section. In view of the present systematic chaos within the Vascoceratidae, the value of this subgenus is questionable.

Plesiovascoceras Spath (type species *Ammonites catinus* Mantell 1822: 195, pl. 22 (fig. 10)) was considered by Wright (in Arkell *et al.* 1957: L419) to show the following characters: 'Evolute, with very depressed whorl section; early whorls with coarse ribs in pairs, interrupted on venter; later whorls almost smooth apart from very large, blunt umbilical or lateral tubercles. Suture as in *Vascoceras*.'

Reeside (1923) described a rich *Plesiovascoceras* fauna from the upper part of the Thermopolis Shale Formation of the Colorado Group in southern Montana. With regard to his material, Reeside (1923: 29) wrote, 'The specimens in hand from Montana are a bit confusing in their relations. The general form, except perhaps for the width of the umbilicus, would permit an assignment to

Fagesia, and the proportions and degree of incision of the suture fit those of *Fagesia* better than those of *Vascoceras*. Moreover, the umbilical tubercles are prominent, and there are traces of the ventral ribs in even the largest specimens. The young whorls, however, show distinctly the umbilical and ventral tubercles of *Vascoceras*, the umbilicus is wider than shown in most of the figured specimens of *Fagesia*, and the suture in every specimen examined shows a pointed first and second lateral lobe, not bifid. The writer therefore assigns the specimens to *Vascoceras* rather than *Fagesia*.'

Freund & Raab (1969: 33) provided the following diagnosis for *Fagesia*:

'Inflated cadicones with large umbilicus. Two to three strong prorsiradiate ribs which cross the venter uninterruptedly, split from each strong umbilical tubercle. Ornament preserved until a late stage. In most species the ribs disappear before the tubercles, and in others, the reverse is true. Outermost whorls usually smooth. Suture deeply incised and rather complicated relative to the common one of the family. Three or four high saddles, the first and second often divided into three branches; lobes narrow, deep, and bifid.'

According to Barber (1957: 131), however, 'Comparison of the diagnoses of *Vascoceras* s.s., *Fagesia* and *Plesiovascoceras* reveals that the differences are of degree rather than of kind, and no single character may be used to separate the genera. The shell-shape and the stage at which the ornament is lost are perhaps the most diagnostic of the characters and therefore young specimens cannot be definitely assigned to a genus. The suture-line is useful in placing doubtful intermediate forms.' As such, therefore, *Fagesia* and *Plesiovascoceras* are separated only on sutural details, a difference which is surely not generic.

The genus *Gombeoceras* Reyment, considered a probable junior synonym of *Thomasites* by Basse (1940) and Freund & Raab (1969), differs from *Vascoceras* in the possession of a row of siphonal tubercles. *Ezilloella* Reyment differs from *Vascoceras* in having a sharply arched to subcarinate venter on the inner whorls and regularly situated bulges on the flanks of the outer whorls. *Neoptychites* Kossmat differs from *Vascoceras* in its extreme involution, and in lacking tubercles at any stage, while *Spathitoides* Wiedmann, considered a synonym of *Vascoceras* s.s. by Freund & Raab (1969), is probably best treated as a subgenus of *Neoptychites*. *Fallotites* Wiedmann is clearly distinguished from *Vascoceras* in the presence of distinct upper and lower ventro-lateral tubercles, while in *Nigericeras* there are also siphonal tubercles.

At present the following subgenera may be recognized within the genus *Vascoceras*:

V. (*Vascoceras*). Compressed to strongly inflated, globose forms in which all ornament is lost on the outer whorls. Inner whorls with prominent swollen umbilical tubercles. Earliest whorls with fold-like ribs which cross the venter. Ribbing quickly becomes effaced across the siphonal line, leaving only ventro-lateral folds.

V. (*Greenhornoceras*). As for *V.* (*Vascoceras*), but more involute and maintaining a quadrate whorl section to large diameters.

V. (*Paravascoceras*). As for *V.* (*Vascoceras*), but umbilical tubercles are lacking at all growth stages. Inner whorls compressed and moderately involute, later becoming somewhat more evolute. Prorsiradiate ribs, uninterrupted across the venter, usually appear at a late growth stage and are generally confined to the ventral region.

V. (*Plesiovascoceras*). Similar to *V.* (*Vascoceras*), but more evolute and with a strongly depressed whorl section. Prominent swollen umbilical tubercles retained to maturity. Early whorls with coarse robust ribbing which weakens, and at later growth stages is entirely effaced across the siphonal line. Ribbing may persist to maturity.

Genus *Vascoceras* Choffat, 1898
Subgenus *Paravascoceras* Furon, 1935
Type species *Vascoceras cauvini* Chudeau, 1909

Vascoceras (*Paravascoceras*) cf. *cauvini* Chudeau, 1909

Figs 6C–H, 35–37

Compare

Vascoceras cauvini Chudeau, 1909: 68, pls 1–3. Furon, 1935: 268, pl. 9 (fig. 17).

Thomasites cauvini (Chudeau) Chudeau, 1921: 463, fig. 1.

Thomasites meslei Chudeau (*non* Pervinquière), 1921: 465, pl 1 (figs 1–2), text-fig. 2.

Vascoceras (*Paravascoceras*) *cauvini* Chudeau, Furon, 1935: 60, pl. 4 (fig. 2), pl. 5 (fig. 1).

Vascoceras (*Paravascoceras*) *cauvini* var. *semiglabra* Furon, 1935: 61, pl. 4 (fig. 3).

Vascoceras (*Pachyvascoceras*) *crassus* Furon, 1935: 58, pl. 3 (fig. 2), text-fig. 17.

Vascoceras (*Paracanthoceras*) *chevalieri* Furon, 1935: 59, pl. 4 (fig. 1), text-fig. 18.

Nigericeras jacqueti Schneegans, 1943: 125, pl. 7 (fig. 1).

Paravascoceras cauvini (Chudeau) Schneegans, 1943: 128, pl. 5 (fig. 2). Freund & Raab 1969: 20, pl. 3 (figs 1–3). Schöbel, 1975: 119, pl. 4 (figs 1–3), pl. 5 (figs 1–4).

Paravascoceras cauvini var. *inflata* Schneegans, 1943: 131.

Paravascoceras cauvini var. *evoluta* Schneegans, 1943: 130, pl. 8 (fig. 2).

Paravascoceras crassus var. *bullata* Schneegans, 1943: 131, pl. 8 (figs 3–4).

Paravascoceras chevalieri (Furon) Schneegans, 1943: 132, pl. 4 (fig. 7).

Broggiiceras humboldti Benavides-Cacères, 1956: 471, pl. 56 (figs 1–3).

Broggiiceras olssoni Benavides-Cacères, 1956: 471, pl. 55 (figs 1–4).

Paravascoceras rumeaui Collignon, 1957: 10, pl. 1 (fig. 2). Freund & Raab, 1969: 21, pl. 3 (figs 4–5), text-fig. 5.

Paravascoceras tavense Freund & Raab (*non* Faraud), 1969: 23, pl. 2 (fig. 9), text-fig. 5.
Paravascoceras crassum (Furon) Freund & Raab, 1969: 24, text-fig. 5.
Paravascoceras cf. *baroicensis* Choffat, Schneegans, 1943: 134, pl. 8 (fig. 1).
Paravascoceras aff. *cauvini* (Chudeau) Barber, 1957: 37, pl. 14 (figs 2–3), pl. 32 (figs 8–9). Collignon, 1965: 21.
Paravascoceras aff. *chevalieri* (Furon) Reyment, 1955: 63, pl. 14 (fig. 1).
Stoliczkaia dispar var. *attenuata* Douvillé, 1931: 29, pl. 2 (fig. 2).
Gombeoceras sp. Cooper, 1972: 248.

Description

Three rather poorly preserved examples, with the recrystallized test preserved, appear to belong here. They show some variation in ornament, but appear to belong to a single species.

Fig. 35. *Vascoceras* (*Paravascoceras*) cf. *cauvini* Chudeau. The holotype of *Stoliczkaia dispar* var. *attenuata* Douvillé (after Douvillé 1931). × 1.

SAM–PCA2816 (Fig. 6C–D) is fragmentary but the shell appears to have been moderately involute, with a quadrate, compressed whorl section and an evenly rounded venter. The umbilical wall is steep, with a subangular umbilical shoulder. The flanks are flattened, converging slightly towards the venter, with maximum width just above the umbilical shoulder. On the outer whorl, the ornament consists of broad fold-like ribs, strongest on the ventro-lateral shoulders but only weakly joined across the venter by faint ribs and growth lines which are convex adorally.

SAM–PCA2727 (Fig. 6E–F) and PCA2796 (Fig. 6G–H) differ from the

above in lacking distinct ventro-lateral folds. Both specimens are moderately involute, slightly less than half the previous whorl being covered, with a compressed, oval whorl section. The umbilicus is rather narrow and fairly deep. The umbilical wall is steep and slightly undercut at the umbilical seam, with a well-rounded shoulder. The flanks are broad and flat, converging slightly towards the evenly rounded venter. Besides very faint growth striae, ribbing is virtually absent. However, SAM–PCA2727 shows a trituberculate venter (on the internal mould only) where the outer shell layer has been removed. The suture line is illustrated in Figure 37.

Measurements

No.	D	H	W	W/H	U
SAM–PCA2816	45	20 (44)	16 (36)	0,80	8 (0,18)
,,	19	7 (37)	7 (37)	1,00	3 (0,16)
SAM–PCA2727	± 42	± 19 (45)	± 14 (33)	0,74	± 10 (0,24)
,,	33	15 (45)	10 (30)	0,67	7 (0,21)
SAM–PCA2796	37	19 (51)	13 (35)	0,68	?

Discussion

Although there are obvious differences between specimens which lack ventro-lateral folds (SAM–PCA2727, 2796) and the ribbed forms (SAM–PCA2816 and Douvillés holotype (Fig. 35)), they are grouped together because of their close similarity in all other respects. This view is supported by Schneegans's (1943) observation that *Paravascoceras* passes through an unornamented stage between

Fig. 36. *Vascoceras* (*Paravascoceras*) cf. *cauvini* Chudeau. Whorl section of SAM–PCA2816. × 1.

20 and 55 mm diameter. The trituberculate venter, on the internal mould only of SAM–PCA2727, probably merely reflects its ancestry (*Pseudocalycoceras*?).

The Angolan material most closely resembles *V.* (*P.*) *cauvini* Chudeau (1909: 67, pl. 1–3), and may possibly be conspecific. Chudeau's holotype, however, is 107 mm in diameter, while Schneegans's (1943) material is of similar size, and consequently they are not directly comparable. Furthermore, the significant ontogenetic changes in morphology undergone by *Paravascoceras* make comparisons even more difficult.

Schöbel (1975) has recently demonstrated the extreme morphological variation to be found within topotype material of *V.* (*P.*) *cauvini*, and the Angolan material easily falls within the intraspecific limits of Chudeau's species. Reserva-

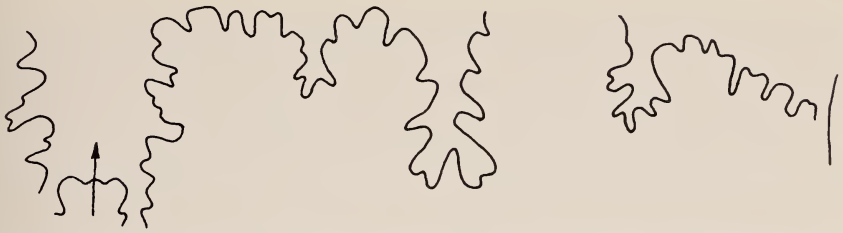

Fig. 37. *Vascoceras* (*Paravascoceras*) cf. *cauvini* Chudeau. Suture-line of SAM–PCA2727 at about 48 mm diameter.

tion as to the identity of the Salinas material stems from the fact that it was collected from surface scree and thus its exact stratigraphic horizon is unknown, together with the acanthoceratid suture-line (Fig. 37) with a broad, bifid lateral saddle.

AGE OF THE FAUNA

The Salinas fauna has yielded many elements in common with both western Europe and North America, and correlation is clearly possible.

In Europe, Juignet & Kennedy (1977) have adopted the following biostratigraphic subdivision of the Cenomanian of southern England and northern France, including the type area of the Cenomanian, Le Mans (Sarthe):

Upper	*Sciponoceras gracile* Zone
	Eucalycoceras pentagonum Zone
Middle	*Acanthoceras jukesbrowni* Zone
	Turrilites acutus Zone
	Turrilites costatus Zone
Lower	*Mantelliceras dixoni* Zone
	Mantelliceras saxbii Zone
	Hypoturrilites carcitanensis Zone

At Salinas there is no sign of the characteristic Upper Albian association of mortoniceratids—*Stoliczkaia–Anisoceras*, nor of the typical Lower Cenomanian faunal assemblage of *Mantelliceras–Sharpeiceras–Hypoturrilites*. Furthermore, the Middle Cenomanian *Acanthoceras–Calycoceras–Turrilites* faunal association recorded from Novo Redondo (Cooper 1973) is also missing at Salinas.

In England, the zone of *Eucalycoceras pentagonum* is characterized by the appearance of *Calycoceras naviculare* while *Acanthoceras hippocastanum* (J. de C. Sowerby), *Eucalycoceras pentagonum* (Jukes-Browne) and *Schloenbachia lymense* Spath are typical. Other important elements of the fauna are *Puzosia* (*Austiniceras*) *austeni* (Sharpe), *Calycoceras* gr. *newboldi* (Kossmat), *Scaphites equalis* J. Sowerby and *Protacanthoceras* spp. Rare components of the fauna include *Calycoceras* (*Lotzeites*) *aberrans* (Kossmat), *Carthaginites* cf. *inornatus* (Collignon), *Euomphaloceras euomphalum* (Sharpe), *Turrilites costatus* Lamarck, *Thomelites sornayi* (Thomel), and *T. prerusticum* (Thomel).

The first appearance of *Metoicoceras geslinianum* (d'Orbigny) marks the base of the *Sciponoceras gracile* Zone. Still present are *Calycoceras naviculare* and *Scaphites equalis*, while *Puzosia* (*Anapuzosia*) *dibleyi* (Spath) appears for the first time. Other forms include '*Pachydiscus*' sp. and *Sciponoceras* sp.

In the '*Metoicoceras gourdoni*' Zone, *M. geslinianum* still occurs, while also present are '*M. gourdoni*' (de Grossouvre), *Allocrioceras annulatum* (Shumard), *E.* (*Kanabiceras*) *septemseriatum* (Cragin), *Tarrantoceras faustum* (Matsumoto & Muramoto), *Sciponoceras gracile* (Shumard), *Pseudocalycoceras angolaense* (Spath) and ?*Puebloites* sp. (W. J. Kennedy pers. comm.).

Horizon A, which in northern France has as its equivalent the Craie à *Terebratella carantonensis* (d'Orbigny), was introduced to cover a poorly known part of the sequence yielding *Sciponoceras* of the *gracile* group and *Neocardioceras* sp., but few other ammonites.

The *Mammites nodosoides* Zone at the base of the classical Turonian (Juignet *et al.* 1973; Kennedy & Juignet 1973) is characterized by the occurrence of *Mammites nodosoides* (Schlotheim) and its varieties, together with the bivalve *Inoceramus* (*Mytiloides*) *labiatus labiatus* (Schlotheim). Other ammonites include *Vascoceras* (*Plesiovascoceras*) *catinum* (Mantell), *Fagesia pachydiscoides* (Spath), *F.* cf. *superstes* (Kossmat), *Metasigaloceras rusticum* (J. Sowerby), *Lewesiceras peramplum* (Mantell) and *Watinoceras?* spp.

There can be little doubt that the bulk of the Salinas fauna finds its equivalents in the fauna of the *Actinocamax plenus* Marls (Jefferies 1962, 1963) and Horizon A (Kennedy & Juignet 1973) in southern England, and in the Sables à *Catopygus obtusus* in northern France.

Uppermost Cenomanian strata are exposed over wide areas of the Western Interior of North America. In Colorado, top Cenomanian strata, referred to a Zone of *Sciponoceras gracile*, are represented by the basal beds of the Bridge Creek Limestone Member. This unit has yielded a rich ammonite fauna (Cobban 1971; Cobban & Scott 1972) comprising the following forms: *Metoicoceras whitei* Hyatt (= *M. gibbosum* Hyatt), *Calycoceras naviculare* (Mantell), *Pseudocalycoceras dentonense* (Moreman) (= *P. angolaense* (Spath)), *Sciponoceras gracile* (Shumard), *Euomphaloceras* (*Kanabiceras*) *septemseriatum* (Cragin), *Allocrioceras annulatum* (Shumard), *Worthoceras gibbosum* Moreman, *W. vermiculum* (Shumard), *Puebloites corrugatus* (Stanton), *Anisoceras plicatile* (J. Sowerby), *Hemiptychoceras reesidei* Cobban & Scott, *Desmoceras* (*Moremanoceras*) *scotti* (Moreman) and the bivalve *Inoceramus pictus* Sowerby. A limestone unit some 6 m higher up has yielded a fauna including *Watinoceras coloradoense* (Henderson), *Ampakabites collignoni* Cobban & Scott, *Neoptychites xetriformis* Pervinquière, *N.* cf. *cephalotus* (Courtiller), *Fagesia* sp., *Mammites* sp., *Baculites* cf. *yokoyamai* Tokunaga & Shimizu, *Puebloites spiralis* Cobban & Scott, *Vascoceras* (*Greenhornoceras*) *birchbyi* Cobban & Scott and the bivalve *Inoceramus labiatus*. The close similarity with the Angolan fauna leaves little doubt as to their contemporaneity.

In Texas, the zone of *Metoicoceras whitei* Hyatt is represented in the Britton

Member of the Eagle Ford Group. Moreman (1942) has listed the following ammonites from this unit: *Tarrantoceras bentonianum* (Cragin), *Pseudocalycoceras angolaense* (Spath) (including *Eucalycoceras dentonense* Moreman, *E. lewisvillense* Moreman, *E. indianense* Moreman and *E. underwoodi* Powell), *Desmoceras* (*Moremanoceras*) *scotti* (Moreman), *Allocrioceras annulatum* (Shumard) (including *A. pariense* (White)), *A. larvatum* (Conrad), *A. dentonense* Moreman, *A.? rotundatum* (Conrad), *Metoicoceras gibbosum* Hyatt (including *M. whitei* Hyatt, *M. acceleratum* Hyatt, *M. kanabense* Hyatt, and *M. ornatum* Moreman), *M. irwini* Moreman, *Worthoceras vermiculum* (Shumard), *W. gibbosum* Moreman, *Euomphaloceras* (*Kanabiceras*) *septemseriatum* (Cragin), *Sciponoceras gracile* (Shumard), *Scaphites brittonense* Moreman, *S. minutus* Moreman, *Protengonoceras planum* Hyatt, *Epengonoceras acutum* Hyatt, *Proplacenticeras cumminsi* (Cragin), *P. pseudoplacenta occidentale* (Hyatt) and *P. stantoni bolli* (Hyatt). Although this list needs revision, and there are a number of apparently endemic taxa within the Texas fauna, there can be no question about its contemporaneity with the Angolan fauna.

A typical uppermost Cenomanian fauna is known (Matsumoto *et al.* 1957; Matsumoto 1959*b*; Matsumoto *et al.* 1969; Matsumoto & Kawano 1975) from the top of unit IIc, middle member of the Mikasa Formation, central Hokkaido, Japan, including *E.* (*Kanabiceras*) *septemseriatum* (Cragin), *Sciponoceras gracile* (= *S. kossmati* (*Nowak*)), *Pseudocalycoceras angolaense* (Spath) (= *Eucalycoceras* sp., Matsumoto *et al.* 1957: 38, pl. 11 (fig. 2)) and *Tarrantoceras faustum* (Matsumoto & Muramoto).

In both north-western Europe (Kennedy 1971; Kennedy & Juignet 1973; Juignet *et al.* 1973) and North America (Cobban & Scott 1972) the faunal association *Sciponoceras gracile–Kanabiceras septemseriatum–Metoicoceras* spp. is considered diagnostic of the uppermost Cenomanian. The writer concurs with these opinions. Records of *Metoicoceras* from the Lower Cenomanian of Madagascar (Collignon 1964) clearly need reinvestigation, while the appearance of this genus in the Lower Turonian of Israel (Freund & Raab 1969) is possibly based upon misidentification. Collignon (1966) recorded *Metoicoceras* from the Lower Turonian of Morocco, but these faunas are almost certainly contemporaneous with the Angolan assemblage.

The occurrence at Salinas of *Watinoceras coloradoense* (Henderson) and *Vascoceras* (*Paravascoceras*) cf. *cauvini* Chudeau suggests a slightly higher faunal horizon (the basal Turonian zone of *Watinoceras coloradoense*) to be present, although as these forms were picked up in surface scree this needs substantiating.

THE CENOMANIAN–TURONIAN BOUNDARY PROBLEM

The exact position of the Cenomanian–Turonian boundary has long been a point of contention. In north-western Europe, it has been variously drawn, on both litho- and biostratigraphic grounds, at below the *plenus* Marls (= *geslinianum* + *gourdoni* Zones) (Thomel 1972, 1973; Jefferies 1962, 1963), some way above the *plenus* Zone (Kennedy 1971; Kennedy & Juignet 1973), and at a still

higher horizon (Berthou & Lauverjat 1974), so as to include a zone of *Vascoceras gamai-mundae* within the Cenomanian.

The type area of the Cenomanian is in the vicinity of Le Mans, Sarthe, north-western France (d'Orbigny 1847), while 'l'etage Turonien' was first recognized (d'Orbigny 1842) along the Cher Valley between Montrichard and Tours, Touraine. This stage was later restricted (d'Orbigny 1847: 270) to those beds containing *Ammonites lewesiensis* (= *Lewesiceras*), *A. peramplus* (= *Lewesiceras*) *A. vielbanci* (= *Mammites* of authors), *A. woollgari* (= *Collignoniceras*), *A. fleuriausianus* (= *Prionotropis* of authors), *A. deverianus* (= *Romaniceras*).

Kennedy & Juignet (1973) have recently shown there to be a considerable overlap between the succession of the type Cenomanian and that of the Turonian stratotype. These authors recognized the following lithostratigraphic and ammonite succession across the Cenomanian–Turonian boundary. From above downwards they are:

(iv) Craie à *Inoceramus labiatus*—characterized by the appearance of *I. labiatus labiatus* Schlotheim and *Mammites nodosoides* (Schlotheim).

(iii) Craie à *Terebratella carantonensis*—in places *Inoceramus* gr. *pictus* J. Sowerby occurs *in situ*, but the only known ammonites are derived Upper Cenomanian forms.

(ii) Sables à *Catopygus obtusus*—yielding a fauna characterized by *Metoiceras gourdoni* (de Grossouvre), *M. geslinianum* (d'Orbigny). *Euomphaloceras* (*Kanabiceras*) *septemseriatum* (Cragin), *Sciponoceras gracile* (Shumard), *Calycoceras naviculare* (Mantell) and *Watinoceras?* sp.

(i) Marnes à *Ostrea biauriculata*—with *Calycoceras naviculare* (Mantell), *Thomelites sornayi* (Thomel), *Eucalycoceras rowei* Spath and *Calycoceras* gr. *newboldi* (Kossmat).

Kennedy & Juignet (1973: 199) were led to conclude that since 'the *Metoiceras gourdoni* Zone is present within the type Cenomanian, where it is represented by the Sables à *Catopygus obtusus*. Their fauna, including key forms such as *M. geslinianum* and *T. carantonensis* were always regarded by d'Orbigny as Cenomanian', that this Zone should be placed in the Cenomanian, and that 'the most convenient level for the base of the Turonian would thus appear to be the base of the classic *Mammites nodosoides*/*Inoceramus labiatus* Zone, defined on its fauna and not on lithology'. Unfortunately, they do not specify what this fauna is, and undoubted Turonian ammonites occur below either of these taxa.

In order to objectively review the Cenomanian–Turonian boundary problem, it is necessary to look at the present biostratigraphical zonation through these two stages. After Wright (in Arkell *et al.* 1957) and Juignet & Kennedy (1977), these are:

Upper Turonian	*Subprionocyclus neptuni*
Middle Turonian	*Collignoniceras woollgari*
Lower Turonian	*Mammites nodosoides*
Upper Cenomanian	*Sciponoceras gracile*
	Eucalycoceras pentagonum

In the classical Turonian of Le Mans, Sarthe, Kennedy & Juignet (1973) recognized a zone of *Mammites nodosoides* only in the Lower Turonian. However, in those parts of the world from where rich and diversified Lower Turonian faunas are known, the base of the Turonian is characterized by strata rich in *Vascoceras* s.s., together with forms of *V.* (*Paravascoceras*), *Nigericeras*, *Gombeoceras*, *Watinoceras*, *Fallotites* and *Fagesia*, while *Mammites* appears for the first time only well above the *Vascoceras* faunas in Israel (Freund & Raab 1969), Nigeria (Reyment 1955; Barber 1957), northern Spain and Portugal (Wiedmann 1959, 1964), and the Western Interior of North America (Cobban & Scott 1972). In Madagascar, *M. nodosoides* is known only from the Middle Turonian 'Zone à *Pseudaspidoceras conciliatum* (Stoliczka)' (Collignon 1965). The relative paucity of fossils within the early Turonian chalk environment of north-western Europe does not allow for the recognition of a detailed biostratigraphical zonation, and it becomes necessary to look elsewhere in the world.

Choffat (1900) subdivided the Upper Cenomanian–Turonian of Portugal into 12 units, numbered alphabetically from C to N. From above downwards they were:

M, N	Limestones with gasteropods
L	Beds with *Fagesia superstes*, *Choffaticeras barjonai*, *Vascoceras durandi* and *Inoceramus labiatus*
I–K	Unfossiliferous limestones and dolomites
H	Limestones which at their summit yield *Fallotites subconciliatus*, *Vascoceras durandi* and *Pseudaspidoceras footeanum*
G	Passage beds lacking in fossils
E–F	Beds with *Vascoceras gamai* and *V. mundae*
D	Beds with the echinoids *Anorthopygus michelini* and *A. orbicularis*, but lacking in ammonites.
C	Beds with *Neolobites vibrayeanus* (= *N. choffati* Hyatt) and *Calycoceras naviculare*

A supposedly characteristic Cenomanian microfauna from Beds E–F led Berthou & Lauverjat (1974) to include a zone of *Vascoceras gamai* and *V. mundae* at the top of the Cenomanian. This was supported by Thomel's (1972) assignment of Choffat's *C. naviculare* to *C. stoliczkai* (Collignon), a species considered by him to be restricted to his zone of *Calycoceras robustum* Thomel, at the base of the Upper Cenomanian. As shown by Cobban (1971) and Kennedy (1971), however, the specimens figured by Choffat (1898: 72, pl. 4 (fig. 6a–b), pl. 6 (figs 1–2)) are true *C. naviculare* (Mantell), of which *C. stoliczkai* is a junior subjective synonym. Consequently, *Calycoceras naviculare* is a relatively long-ranging species which is known from many levels in the Upper Cenomanian and its occurrence some way below strata with *Vascoceras* is not considered significant.

The problem of whether or not to include a zone of *Vascoceras gamai* Choffat at the top of the Cenomanian is difficult. Like Kennedy & Juignet (1973), the writer prefers to regard the genus *Metoicoceras* as being restricted to an

horizon very high in the Cenomanian. Its relationship to the vascoceratid faunas is thus critical.

In Israel, Freund & Raab (1969: 78) record *Metoicoceras* cf. *whitei* Hyatt, unfortunately without figure or proper description, from their Zone 4 of *Choffaticeras securiforme* (Eck). If correctly identified, this could provide strong supporting evidence for the inclusion of at least part of the vascoceratid faunas within the Cenomanian. It seems more likely, however, that the Israeli form may be a misidentification of a typically Lower to Middle Turonian *Spathites* (*Spathites*) or *S.* (*Jeanrogericeras*).

From the Puentedey valley, near Soncillo, Villamartin, Turzo (Burgos Province), northern Spain, Wiedmann (1964) gave a detailed succession across the Cenomanian–Turonian boundary. From above downwards this was:

(vii) 6 m of blue marls with *Fallotites* (*Ingridella*) cf. *malladae* (Fallot), *Wrightoceras mirabile* (Pervinquière), *W. llarenai* (Karrenberg), *Hoplitoides* sp., *Proromaniceras pseudodeverianum* (Jimbo), *Vascoceras* (*Paravascoceras*) *grossouvrei* (Choffat), *Spathites laevis* (Karrenberg), *Jeanrogericeras revelieranum* (Courtiller), *Schindewolfites inaequicostatus* Wiedmann.

(vi) 10 m of blue marls with *Choffaticeras quaasi* (Peron), *C. pavillieri* (Pervinquière), *Vascoceras durandi* (Peron), *Spathites* cf. *laevis* (Karrenberg), *Fallotites* (*Fallotites*) sp.

(v) 2 m of blue marls with *F.* (*Fallotites*) cf. *subconciliatus* (Choffat).

(iv) 5 m of blue marls with *Vascoceras* (*Plesiovascoceras*) *fagesioides* Wiedmann, *Vascoceras* cf. *gamai* Choffat, *Watinoceras* sp. and *Metoicoceras* cf. *swallovi* (Shumard).

(iii) 4 m of marls with *M. swallovi* (Shumard), *M.* cf. *swallovi* (Shumard), *M.* cf. *whitei* Hyatt, '*Parapuzosia*' cf. *gaudama* (Forbes).

(ii) 2 m of marls and limestones with *Metoicoceras muelleri* Cobban and *Rhynchostreon suborbiculatum* (Lamarck).

(i) 2 m of marls with *Neolobites brancai* Eck, *N.* cf. *vibrayeanus* (d'Orbigny), *N. choffati* Hyatt, *N.* cf. *schweinfurthi* Eck, *Calycoceras naviculare* (Mantell), *Pseudocalycoceras haugi* (Pervinquière).

The importance of the Spanish sections cannot be overestimated, since this is one of the few areas where rich *Metoicoceras* and vascoceratid faunas have been described from the same section. It is also very significant that the vast majority of *Metoicoceras* occur immediately below the vascoceratids. However, from his Lower Turonian Zone 2, Wiedmann (1964) records *Metoicoceras* cf. *swallovi* (Shumard) in association with *Vascoceras* (*Vascoceras*) cf. *gamai* Choffat and *Vascoceras* (*Plesiovascoceras*) *fagesioides* Wiedmann. It is, unfortunately, not clear whether *Metoicoceras* occurs side by side with the vascoceratids or at a slightly lower level in the 5 m section. Consequently, once again unequivocal evidence for the overlap of the *Metoicoceras* and *Vascoceras* faunas is at present lacking.

Cobban & Scott (1972) have recently recorded faunas across the

Cenomanian–Turonian boundary from the Bridge Creek Limestone Member near Pueblo, Colorado. A typical *Sciponoceras gracile* faunal assemblage, placed as the uppermost zone in the Cenomanian, occurs associated with the bivalve *Inoceramus pictus* Sowerby. Some 3 m higher up, a 15 cm limestone bed has yielded *Vascoceras* (*Greenhornoceras*) *birchbyi* Cobban & Scott, *Watinoceras coloradoense* (Henderson), *Puebloites spiralis* Cobban & Scott and a *Fagesia* sp., in association with the typically Turonian *Inoceramus labiatus* Schlotheim. Also significant is the fact that *Mammites nodosoides* (? *non* Schlotheim) first appears some 1,5 m above strata with *Vascoceras.*

The only continuous section through the lower part of the Lower Turonian of Nigeria is at Pindiga (Barber 1957) where some 30 m of shales, sandy mudstones and sandstones, lacking in ammonites, rest conformably upon terrestrial beds and are overlain by about 80 m of fossiliferous strata, Barber (1957: 60) gave the following succession from above downwards:

(viii) About 40 m of shales with thin nodular horizons yielding the ammonites *Pseudotissotia* (*Bauchioceras*) *nigeriensis nigeriensis* (Woods), *P.* (*B.*) *n. tabulata* Barber and *Eotissotia simplex* Barber.

(vii) 0,8 m of rubbly limestone with *Vascoceras globosum* (Reyment), *Gombeoceras gongilense gongilense* (Woods), *G. g. lautum* Barber, *G. g. tectiforme* Barber, *Paramammites* sp. and *Nigericeras* sp.

(vi) 4 m of barren shale.

(v) 0,22 m of crystalline limestone with *Vascoceras nigeriense* Woods, *V. ellipticum* Barber, *V. polygonum* Barber, *V.* (*Paravascoceras*) *costatum* (Reyment), *Gombeoceras gongilense* (Woods), *G. g. costatum* Barber.

(iv) About 60 m of unfossiliferous shales.

(iii) 2 m of nodular limestone with *Vascoceras bulbosum* (Reyment) and *V. depressum* Barber.

(ii) Some 12 m of barren shale.

(i) 0,3 m of crystalline limestone with *Vascoceras bulbosum* (Reyment) and *Epengonoceras dumbli* (Cragin).

It is of interest to note Barber's (1957: 61) observation that 'The fauna associated with the Salmurian ammonites here described has many members which may occur in the Cenomanian. It would appear therefore that the Nigerian Salmurian occurs close to the Cenomanian–Turonian boundary.' Moreover, *Epengonoceras dumbli* is known only from the Middle and Upper Cenomanian in Texas and the Western Interior.

From the Cerro del Macho in Coahuila, Mexico, Böse (1918) described a rich upper Cenomanian–Lower Turonian fauna. Böse (1918: 183) gave the following section, from above downwards:

(iii) 5–6 m of hard gray limestone with *Vascoceras* (*Paravascoceras*) *angermanni* Böse, *V.* ex aff. *gamai* Choffat, *Neoptychites* aff. *xetriformis Pervinquière*, *Hoplitoides* aff. *mirabilis* Pervinquière and *Inoceramus labiatus* Schlotheim.

(ii) 2,5 m of bluish-gray marls with *Fallotites mohovanensis* (Böse), *Pseudaspidoceras flexuosum* Powell, *Pseudaspidoceras* aff. *pedroanum* White, *Vascoceras* aff. *adonense* Choffat, *Fagesia haarmanni* Böse and *Fagesia pervinquieri* Böse.

(i) 2 m of yellow and reddish marls and limestones with *Metoicoceras* aff. *whitei* Hyatt, *M. boesei* Jones and *Exogyra* (*Costagyra*) cfr. *olisiponensis* Sharpe.

The above section once again clearly shows *Metoicoceras* to occur immediately below what have always been regarded as typical Lower Turonian ammonites.

It becomes obvious, therefore, that for both biostratigraphic correlation and in order to clarify the Cenomanian–Turonian boundary problem, it is important to introduce a zone beneath the classical Lower Turonian zone of *Mammites nodosoides*. In the Western Interior, Cobban & Scott (1972) have recognized a basal Turonian zone of *Watinoceras coloradoense*. The wide geographic distribution of this species, together with the fact that *Watinoceras* also appears to mark the base of the Turonian in Angola, Spain and possibly the Anglo-Paris basin, all seem to support its usage as the basal Turonian index fossil. There can be little doubt that with the rich faunas available, together with a better understanding of vascoceratid taxonomy and stratigraphy, a far more refined zonal scheme for the Lower Turonian will eventually be possible. At present only the following Upper Cenomanian–Lower Turonian ammonite zones appear to be of world-wide importance:

Lower Turonian	*Mammites nodosoides*
	Watinoceras coloradoense
Upper Cenomanian	*Sciponoceras gracile*
	Eucalycoceras pentagonum

These are assemblage zones, and may be briefly diagnosed as follows:

Eucalycoceras pentagonum Zone—typical elements of the fauna include *E. pentagonum* (Jukes-Browne), *Acanthoceras hippocastanum* (J. de C. Sowerby), *Protacanthoceras* of the *bunburianum–compressum* group, *Thomelites* spp., *Pseudocalycoceras harpax* (Stoliczka), *Euomphaloceras euomphalum* (Sharpe), *Calycoceras* (*Newboldiceras*) spp., *C.* (*Calycoceras*) *boulei* Collignon and *C.* (*C.*) *naviculare* (Mantell).

Sciponoceras gracile Zone—characterized by *S. gracile* (Shumard), *Metoicoceras* spp., *Euomphaloceras* (*Kanabiceras*) *septemseriatum* (Cragin), *Pseudocalycoceras angolaense* (Spath), and *Calycoceras naviculare* (Mantell), together with *Puzosia* (*Austiniceras*) *austeni* (Sharpe), *P.* (*Anapuzosia*) *dibleyi* (Spath), *Desmoceras* (*Moremanoceras*) *scotti* Moreman, *Allocrioceras* spp., and *Tarrantoceras faustum* (Matsumoto & Muramoto).

Watinoceras coloradoense Zone—the faunas of this zone are not yet well differentiated from those of the overlying *nodosoides* Zone. However, *Watinoceras*

	Herein	Juignet & Kennedy (1977)	Berthou & Lauverjat (1975)	Kennedy & Juignet (1973)	Thomel (1972)
LOWER TURONIAN	*Mammites nodosoides*	*Mammites nodosoides*	*Fagesia superstes* *Pachyvascoceras douvillei—durandi* *Couche de passage*	*Mammites nodosoides*	*Mammites nodosoides*
	Watinoceras coloradoense				*Fagesia superstes*
UPPER CENOMANIAN	*Sciponoceras gracile*	*Sciponoceras gracile*	*Vascoceras gamai—mundae* *Niveau à Anorthopygus michelini*	Horizon A *Metoicoceras gourdoni* *Metoicoceras geslinianum*	*Calycoceras naviculare*
	Eucalycoceras pentagonum	*Eucalycoceras pentagonum*	*Neolobites vibrayeanus*	*Calycoceras naviculare*	*Calycoceras crassum* *Calycoceras robustum*

	Herein	Cobban & Scott (1972)	Freund & Raab (1969)	Wiedmann (1959)	Barber (1957)
LOWER TURONIAN	*Mammites nodosoides*	*Mammites nodosoides*	*Choffaticeras luciae* *Choffaticeras quaasi* *Choffaticeras securiforme* *'Vascoceras' pioti*	*Wrightoceras munieri* *Ingridella malladae* *Paramammites? saenzi* *Fallotites subconciliatus*	*Kamerunoceras eschii* *Bauchioceras nigeriensis* *Paravascoceras costatum*
	Watinoceras coloradoense	*Watinoceras coloradoense*	*Paravascoceras cauvini* *Kanabiceras* sp.	*Vascoceras gamai* *Metoicoceras swallovi*	*Vascoceras bulbosum*
UPPER CENOMANIAN	*Sciponoceras gracile*	*Sciponoceras gracile*	*Neolobites* sp. *Calycoceras* sp.	*Metoicoceras muelleri*	
	Fucalycoceras pentagonum	*Dunveganoceras albertense* *Dunveganoceras conditum* *Dunveganoceras pondi*		*Neolobites choffati* *'Protacanthoceras' jacobi*	

Fig. 38. Upper Cenomanian–Lower Turonian biostratigraphical zonation proposed herein, compared with previously erected schemes.

coloradoense (Henderson) and *Vascoceras* (*Paravascoceras*) *cauvini* Chudeau appear to be typical, possibly also with species of *Pseudaspidoceras*, *Nigericeras*, *V.* (*Vascoceras*) of the *gamai–mundae* group, *V.* (*Plesiovascoceras*), *Fagesia*, *Neoptychites* and *Fallotites*.

Mammites nodosoides Zone—it is from this zone that most of the classical Lower Turonian ammonites have been collected, and further subdivision will undoubtedly prove possible. Typical elements of the fauna include *M. nodosoides* (Schlotheim), together with species of *Choffaticeras*, *Fallotites*, *Hoplitoides*, *Neoptychites*, *Kamerunoceras*, *Schindewolfites*, *Pseudotissotia* (*Wrightoceras*), *Thomasites*, *Vascoceras*, *Fagesia*, *Spathites* (*Spathites*), *S.* (*Jeanrogericeras*) and *Donenriquoceras*.

As can be seen from Figure 38, there has been considerable debate as to the position of the Cenomanian–Turonian boundary. The writer prefers to include the *Sciponoceras gracile* Zone as the uppermost biostratigraphical unit in the Cenomanian for the following reasons:

(i) A typical Cenomanian acanthoceratinid fauna, including *Calycoceras*, *Pseudocalycoceras*, *Tarrantoceras*, *Metoicoceras* and possibly *Protacanthoceras* persist into this zone.
(ii) The diagnostic Upper Cenomanian *Calycoceras naviculare* (Mantell) is abundant in the *gracile* Zone.
(iii) The persistence of the typically Cenomanian *Inoceramus pictus* into this zone.
(iv) The association of the diagnostic Lower Turonian *Inoceramus labiatus* with most vascoceratid faunas, and its absence from the *gracile* Zone.

PALAEOGEOGRAPHIC SIGNIFICANCE

The Salinas fauna is part of the characteristic, world-wide (Fig. 39), uppermost Cenomanian *Sciponoceras gracile* faunal assemblage. Members of this fauna are widely distributed in the Western Interior of North America (Cobban & Scott 1972), extending as far north as Montana (Cobban 1953) and as far south as Texas (Moreman 1942; Powell 1963*b*) and Mexico (Böse 1918; Jones 1938). In the Anglo-Paris basin, the association of *Sciponoceras gracile–Kanabiceras septemseriatum–Metoicoceras* spp. is known over wide areas (Jefferies 1962, 1963; Juignet *et al.* 1973). In Spain and Portugal (Karrenberg 1935; Wiedmann 1959, 1964) a rich *Metoicoceras* fauna is reported from the top of the Cenomanian, but the exact constituents are at present poorly known.

Metoicoceras is also known from Morocco (Collignon 1966), Israel (Avnimelech & Shoresh 1962), Nigeria (Reyment 1955), Brazil (Reyment & Tait 1972*a*) and Madagascar (Collignon 1964), but the stratigraphy of these areas is poorly understood, and the associated ammonite faunas are not known. The record of this genus from southern India (Sastry & Matsumoto 1967) is based upon the closely allied Lower Turonian *Spathites* (*Jeanrogericeras*). Enigmatic is the almost complete absence of *Metoicoceras*, save for the Madagascar occurrence,

Fig. 39. Palaeogeographic reconstruction of Laurasia and the southern continents during the latest Cenomanian–earliest Turonian showing distribution of *Sciponoceras gracile* Zone and *Watinoceras coloradoense* Zone fauna. m = *Metoicoceras* spp., k = *Euomphaloceras* (*Kanabiceras*) *septemseriatum* (Cragin), c = *Calycoceras naviculare* (Mantell), s = *Sciponoceras gracile* (Shumard), p = *Pseudocalycoceras angolaense* (Spath), d = *Puzosia* (*Anapuzosia*) *dibleyi* (Spath), w = *Watinoceras* spp.

from the Indo-Pacific realm. Its absence along the east coast of Africa, however, is related to the absence of strata of this age (Cooper 1974).

Sciponoceras gracile (Shumard) (including *S. kossmati*) is recorded from California (Anderson 1958; Matsumoto 1959*a*) in association with *E.* (*K.*) *septemseriatum* and *C. naviculare*, as also in Japan (Matsumoto & Obata 1963) where other elements of the fauna include *Tarrantoceras* and *Pseudocalycoceras*. Elements of the *gracile* Zone fauna recorded from southern India (Stoliczka 1865; Kossmat 1895) include the relatively long-ranging *C. naviculare* and *S. gracile*, but the exact associations are not known; *Metoicoceras* and *Kanabiceras* are unrecorded and it is possible that uppermost Cenomanian strata are absent.

Thus, a typical *gracile* Zone fauna is known from as far afield as North America (California, Western Interior, Texas, Mexico), South America (Brazil), Africa (North Africa, Morocco, Nigeria, Angola), the Middle East, France, England, India? and Japan. Its absence from the Arctic and austral realms may be due to absence of strata of this age, although it is more likely that there was an ecological barrier (? cold water). A *gracile* Zone fauna appears, therefore, to have attained a virtually cosmopolitan distribution within the equatorial and temperate waters of the late Cenomanian oceans.

A number of authors (Reyment 1969, 1971*a*, 1972, 1973; Reyment & Tait 1972*a*, 1972*b*) have concluded from a study of Cretaceous ammonite distributions in the sedimentary basins surrounding the South Atlantic that a continuous connection between the North and South Atlantic Oceans was not established until the end of the Lower Turonian. In this respect the position of Angola on the initial line of rifting of the Africa–South America plates is critical.

The occurrence of a typical uppermost Cenomanian faunal assemblage from Salinas, virtually identical to similar faunas in North America and western Europe, indicates this seaway to have been open prior to the beginning of the Turonian (Kennedy & Cooper 1975). However, since the uppermost Cenomanian represents a period of eustatic transgression (Cooper 1974), faunal interchange could have occurred merely by flooding of the hypothetical Nigeria–Pernambuco connection. In this respect, the Middle Cenomanian (*Turrilites costatus* and *T. acutus* Zones) fauna recorded from Novo Redondo (Cooper 1973) is also of little help, since this period may also have been an episode of eustatic transgression (Hart & Tarling 1974). To determine the dating of the final break between Africa and South America, i.e. the establishment of a continuous marine connection, it is important to study the faunas of regressive episodes, when exposure of land-bridges, and hence barriers to faunal migration, are most likely to have occurred. The uppermost Albian (*dispar* Zone) faunas provide this opportunity. Whilst the *dispar* Zone fauna of Angola is poorly documented, it is extremely rich and includes the following European species: *Anisoceras armatum* (J. Sowerby), *A. perarmatum* Pictet & Campiche, *Stoliczkaia clavigera* Neumayr, *Mortoniceras* (*Durnovarites*) *perinflatum* (Spath), *M.* (*D.*) *subquadratum* Spath, *Cantabrigites curvatum* Renz, *Mariella gresslyi* (Pictet & Campiche), and possibly

also the Texas mortoniceratinid genus *Drakeoceras* (Cooper 1977). The latest Albian faunas of Angola are, therefore, virtually identical to similar faunas in western Europe at a time of world-wide eustatic regression, which would seem to indicate continuous faunal interchange between the two areas. This suggests that the final rifting between the African and South American plates took place sometime prior to the end of the Albian.

SUMMARY

The type locality of the classic Salinas fauna described by Douvillé was revisited and new material collected. The very high Cenomanian age of the fauna, suspected by previous authors, was confirmed and shown to form part of the world-wide *Sciponoceras gracile* faunal assemblage. The presence of *Watinoceras* and *V.* (*Paravascoceras*) in surface scree at this locality suggests the presence of basal Turonian strata. The geological section was measured and the succession is interpreted as a typical transgressive sequence.

The problem of the Cenomanian–Turonian boundary is reviewed, and Cobban & Scott (1972) are followed in drawing it between the zones of *Watinoceras coloradoense* above and *Euomphaloceras* (*Kanabiceras*) *septemseriatum* below.

Within the family Acanthoceratidae, the new subfamily Euomphaloceratinae is erected to incorporate the following taxa: *E.* (*Euomphaloceras*), *E.* (*Kanabiceras*), *Schindewolfites*, *Kamerunoceras*, *Yubariceras*, *Romaniceras*, *Obiraceras*, *Shuparoceras* and tentatively also *Tunesites*.

The full faunal list from Salinas now reads:

Calycoceras (*Calycoceras*) *naviculare* (Mantell) (= *Acanthoceras borgesi* Douvillé)
Pseudocalycoceras angolaense (Spath) (= *Lyelliceras lyelli* Douvillé *non* Leymerie)
Pseudocalycoceras aff. *haugi* (Pervinquière)
?Protacanthoceras spp.
Tarrantoceras sp. juv. indet.
Euomphaloceras (*Kanabiceras*) *septemseriatum* (Cragin) (= *Prionotropis echinatus* Douvillé)
Watinoceras coloradoense (Henderson)
Metoicoceras gibbosum Hyatt (= *Pulchellia caicedoi* Douvillé *non* Karsten)
Gaudryceras (*Gaudryceras*) *isovokyense* Collignon
Anagaudryceras cf. *cassisianum* (d'Orbigny) (= *Gaudryceras salinarium* Douvillé)
Tetragonites aff. *blaisoni* Collignon
Desmoceras (*Pseudouhligella*) aff. *ezoanum* Matsumoto (= *Desmoceras toucasi* Douvillé *non* Jacob)
?Proplacenticeras sp. (= *Knemiceras uhligi* Douvillé *non* Choffat)

Puzosia (*Anapuzosia*) *dibleyi* (Spath) (= *Puzosia matheroni* Douvillé *non* d'Orbigny)
Puzosia (*Austiniceras*) *intermedia orientalis* Matsumoto
Sciponoceras gracile (Shumard)
Vascoceras (*Paravascoceras*) cf. *cauvini* Chudeau (= *Stoliczkaia dispar* var. *attenuata* Douvillé)

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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order .e.g.:

Family **Nuculanidae**

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
comma separates author's name and year
semicolon separates more than one reference by the same author
full stop separates references by different authors
figures of plates are enclosed in parentheses to distinguish them from text-figures
dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype
SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

MICHAEL R. COOPER

UPPERMOST CENOMANIAN–BASAL TURONIAN AMMONITES FROM SALINAS, ANGOLA